THE UNDERGROUND ORGANS OF HERBAGE GRASSES

by

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Bulletin No. 44
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Hurley, Berkshire

COMMONWEALTH AGRICULTURAL BUREAUX

THIS book provides a comprehensive account of the roots, rhizomes, corms, bulbs and leaf bases of herbage grasses. A description of their morphology, anatomy, life history and chemical composition is followed by a discussion of the effects of environmental factors and farming practices upon their growth, particular emphasis being placed on the relationship between the underground organs and the growth of herbage.

The decay of the underground organs and their effect on the soil are dealt with.

Methods used in studying these organs are also reviewed.

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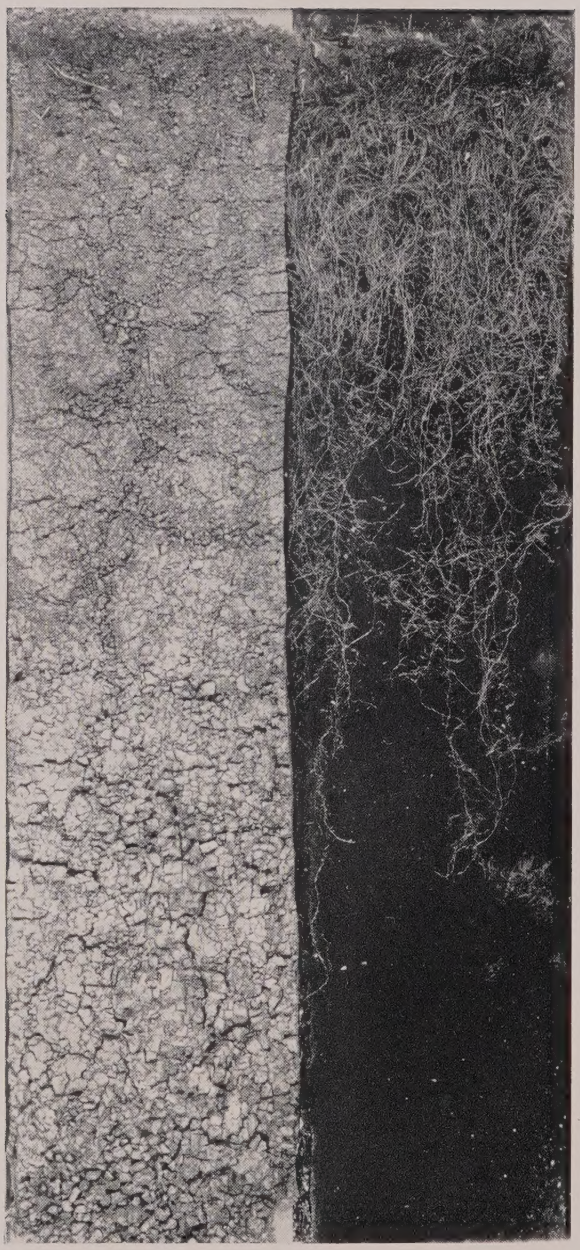

Soil profile and the root development of a grass sward. A river-basin clay soil in the Netherlands. (*Photograph provided by the Landbouwproefstation en Bodemkundig Instituut T.N.O. Groningen, Netherlands*)

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INTRODUCTION

A grass plant may be conveniently divided into roots and shoots. The functions of the shoot system are chiefly photosynthesis and sexual reproduction; those of the root system are anchorage, absorption of water and minerals, and the storage of food reserves. The shoot system is characterized by being mainly above ground while the root system is below. Certain organs, e.g. rhizomes, stolons, corms, and leaf-bases, belong morphologically and anatomically to the shoot system, but are akin to the root system in that they act as storage organs for food reserves, and are normally found, at least partially, underground.

The object of this bulletin is to review the literature concerned with the underground organs of herbage grasses, i.e. the roots, rhizomes, corms etc. of grasses valued for their foliage. A consideration of the growth of these underground organs without reference to the above-ground parts would be unjustifiable because, under natural conditions, all parts of a plant are mutually dependent upon one another. Therefore, the growth of above-ground organs in relation to those underground has been discussed in the appropriate chapters.

In the first part of this bulletin the morphology, anatomy, chemical composition and life histories of the underground organs are reviewed. The second part deals with the environmental factors which influence the growth of these organs, while the third part is concerned with their decomposition and their influence on the soil in which they grow. The length at which any one subject has been treated has depended largely upon the amount of information available on that topic, and not solely upon its importance. Material outside the scope of the work, as indicated by the title, has been excluded, because it was thought that to include it would result in too great a mass of facts being presented in one publication, without adequate detail, and might lead to conclusions which were not strictly applicable to the species indicated by the title.

Such general conclusions as were thought justifiable from the evidence on a particular subject have been given within the first few sentences of the section dealing with that topic. When the evidence did not justify conclusions, no summaries have been attempted because these would be frequently more misleading than helpful, since they would cause conflicting results to be considered without full knowledge of the experiments from which they were obtained.

The agricultural interest in this work depends upon the part the underground organs of grasses play in the production of herbage and the improvement of soil fertility. These are the two major functions of the ley in a system of alternate husbandry. The improvement of soil fertility by grass is mainly a result of the action which the grass roots have upon the soil, first when living, later when decayed.

PART I

DESCRIPTION OF UNDERGROUND ORGANS

CHAPTER 1

SEMINAL ROOTS

Grasses possess two distinct root systems. The primary, or seminal, root system consists of a small number of main roots and their branches. The young plant is, for a time after germination, entirely dependent upon this root system for water and nutrients. The second root system develops from the lower nodes of the shoot.

The seminal root system originates from

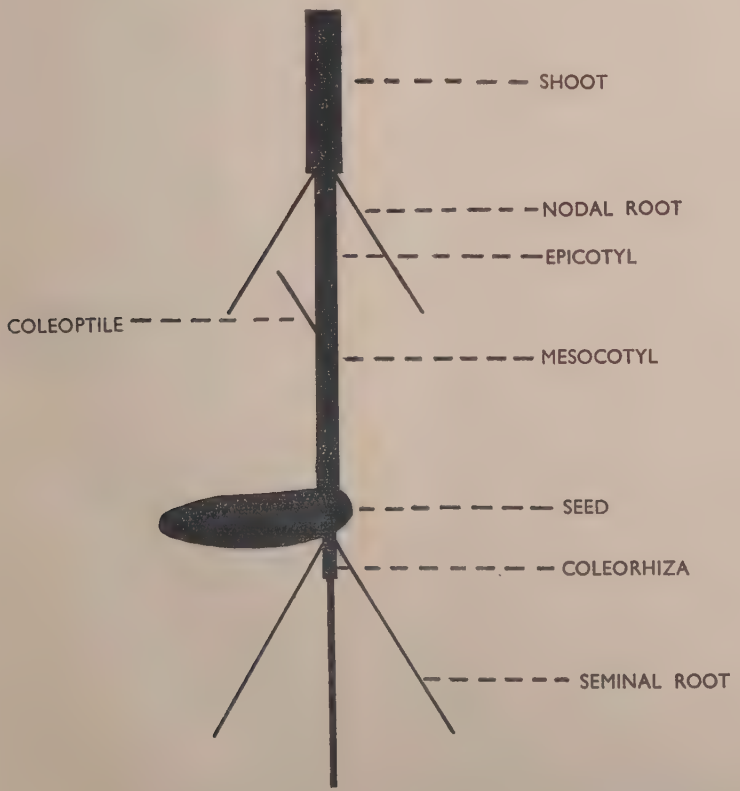


Fig. 1. Schematic drawing of a young grass seedling. Mesocotyl and epicotyl shown elongated to equal lengths. All details described in the text not necessarily illustrated.

initials in the seed (Guttenberg, Heydel and Pankow, 1954). The first part of the root system to emerge from the seed on germination is the coleorhiza. This later forms an integument over the proximal portion of the first seminal root. The coleorhiza of *Phleum pratense* and of *Poa pratensis* was stated by Nishimura (1922) to protect the root, to absorb water and nutrients, and to be capable of functioning for a long time (over 30 days). Paškov (1951) was of the opinion that these conclusions applied to other members of the Gramineae. Nishimura (1922), working with *Phleum pratense* and *Poa pratensis*, Schwartz (cited by Haberlandt, 1914), working with *Panicum miliaceum* and *Setaria italica*, and Haberlandt (1914) working with *Briza minor*, noted that the coleorhiza produced hairs analagous to root hairs.

The number of seminal roots produced by a seed is, apparently, largely a genetic function. These roots normally function for several weeks, but, in certain circumstances, they may function for several months. They are very efficient, and a plant may make considerable growth with its seminal roots as the only functional part of its root system. Each root is capable of considerable branching and growth in length.

The number of seminal roots produced per plant was found by Pavlychenko (1942) to vary within narrow limits for each species. The large-seeded annual species developed a larger number than the small-seeded perennial species. In his view, the number of seminal roots produced was largely a genetic character, and therefore, more or less constant, while the number of nodal roots depended mainly upon environmental conditions. The average number of seminal roots he found on month-old seedlings of *Agropyron cristatum* was 2·4, on *Bromus inermis*, 2·0, and on *Agropyron pauciflorum*, 1·1. Robocker, Curtis and Ahlgren (1953) stated that *Elymus canadensis* developed four, while *Andropogon gerardii*, *Panicum virgatum* and *Bouteloua gracilis* developed only one.

Nevertheless, in Pavlychenko's experiment there was some variation in the number of seminal roots produced by plants of the same species and he concluded that too many seminal roots were a disadvantage, as plants with more than the normal number lacked vigour and soon died. This may have been due to a large number of roots exhausting the limited food reserves before the leaves were sufficiently developed to provide nourishment. The number of seminal roots and the survival of the plant were also related to the depth from which the seedling emerged. Most seedlings emerging from a depth greater than 0·5 in. produced an excess of seminal roots and perished within 2 to 4 weeks. Likewise, plants from seeds which had germinated on the surface of the soil had more than the usual number of seminal roots, were weak and died during their first month. Seeds that germinated between the surface of the soil and a depth of 0·5 in. produced vigorous plants with the normal number of seminal roots.

The early growth of the seminal roots of *Buchloë dactyloides* has been described by Webb (1941). During the first week after growth started they grew at the rate of 1 cm. per day, but ceased growth after attaining a length of 25 to 35 cm. Lateral roots were sent out about 9 days after the seed was planted. The seminal root was well clothed with root hairs and the growing tip (the last 2 cm.) was white in colour. In *Bouteloua gracilis*, Riegel (1941) observed that after the single seminal root had broken through the coleorhiza it elongated at the rate of approximately 0·5 cm. for the first 4 or 5 days, reaching a length of 2 or 3 cm. in 5 to 7 days. Lateral roots appeared at this stage, the main root still continuing to elongate. The main root was covered with root hairs, but with the appearance of lateral roots these hairs ceased to function except near the tip, where, for the space of 1 to 4 cm., no laterals had yet developed. There were 8 to 10 lateral roots on each centimetre of main root with the exception of the tip region. As these lateral roots increased in length, tertiary rootlets, covered with root hairs, developed from them, usually 5 to 10 days after they had started elongating. The main seminal root grew to a length of 6 to 14 cm. and remained active for 4 to 6 weeks. It was about 0·15 mm. in diameter throughout most of its length while young and growing, but decreased in diameter as it became less active.

Descriptions of the development of the seminal root systems of 14 species of perennial grasses were given by Weaver and Zink (1945). The species studied comprised 10 species native to, and 4 species of economic importance introduced into, Nebraska. The seminal roots were 6 to 10 inches deep 21 days after sowing. At this stage there were 1 to 4 nodal roots, but rarely a tiller. Twenty days later, when the grasses were mostly 8 to 10 inches tall, the seminal root depth was 7·5 to 27 inches, and the nodal roots were often equally

deep. Seminal roots were usually very fine, 0·3 mm. or less in diameter. The degree of branching and the length of the branches varied greatly among the species, but nearly all were profusely branched. Little or no decortication of the main root had occurred at this stage in eight species, but in six species the cortex remained only on the distal end. With one exception, the cortex of the branches was practically intact. (p. 8).

After 53 to 74 days, when the plants were 5 to 16 inches high, there were many deeply penetrating nodal roots and numerous tillers one-half to two-thirds the height of the parent culm. Seminal root depth was 10 to 24 inches. On the smaller root branches, and usually on the larger ones, the cortex was intact, but it had sloughed off from some of the main seminal roots. After 90 to 123 days, when the grasses were 9 to 19 inches tall and two species had flowered, the seminal roots, despite 6 to 60 nodal roots, extended deeply, frequently to a depth of 24 in. The cortex was missing from one-third to two-thirds of the root surface.

Describing the growth of *Eragrostis curvula*, Crider (1945) stated that the seminal roots functioned for some three to four weeks before the vegetative culm and nodal roots developed, which they both did at the same time.

In the normal course of events the seminal roots appear to function for a considerable time. Riegel (1941) was of the opinion that those of *Bouteloua gracilis* functioned for 4 to 6 weeks, while Stuckey (1941) gave the period as 6 to 8 weeks for 10 species of temperate grasses, and Pavlychenko (1942) a maximum of 2 months for the perennial grasses he studied. The branched seminal root of *Lolium perenne* was stated by Rappaport (1938) to be still growing when 10 weeks old. Weaver and Zink (1945) found, in their experiment, that the seminal roots of plants were alive and active after 3·5 to 4 months and suggested that under field conditions they may be active throughout the first summer after spring sowing. Seminal roots of *Andropogon furcatus* were found by Stoddart (1935) all to be alive and active when 18 months old, while some were still functioning when 2 years old. According to Kokkonen (1931b), the seminal roots of *Dactylis glomerata* generally die in their second summer.

The life of the seminal root of *Bouteloua curtipendula*, according to Olmsted (1941, 1942), may be lengthened by lack of water, its rate of development being retarded by the same circumstances. The penetration of these roots, in his experiment, was least in the plants receiving water most frequently in the form of precipitation; but, on these roots, numerous laterals were produced in the upper 2 cm. of soil, a contrast to their absence in other plants grown where the surface soil dried rapidly. Normally, these roots appeared to become non-functional when 6 to 10 weeks old. After 4 months, the roots of those plants receiving only a small amount of water were still alive, and, in individual plants, their length and degree of branching showed a strong negative correlation with the number of functional nodal roots. In some cases they were the only functional part of the root system. The imposition of a period without water, if not too severe, probably also tended to prolong the life of these roots. These observations are supported by those of Glendening (1941) on *Heteropogon contortus*. Salonen (1951) noted that the length of life of the seminal roots was greater in grasses grown under a nurse crop than those grown alone, the former being affected by drought whereas the latter were not.

An experiment was carried out by Yates and Jacques (1953) in an attempt to ascertain the relative importance of the seminal and nodal root systems of *Lolium perenne*. The technique of the experiment was, in the appropriate treatments, to amputate the seminal roots 5 weeks after sowing. The nodal roots were amputated 4 weeks after sowing and thereafter at 10-day intervals. The treatments were as follows:—

Control.
Primary seminal root amputated.
Lateral seminal roots amputated.
Nodal roots amputated.
Primary and lateral seminal roots amputated.
Nodal and lateral seminal roots amputated.
Nodal and primary seminal roots amputated.

The plants whose nodal and primary seminal roots were amputated died within a few days of the operation, the lateral seminal roots which were left being unable to support the plants. Two other treatments, amputation of the nodal roots with the seminal roots left intact and amputation of the nodal and the lateral seminal roots, resulted in a less immediate death of the plants; some plants which underwent these treatments survived up to 112 days. Plants receiving the 4 remaining treatments were still alive at the termination of the experiment after 147 days. The application of super-

phosphate did not affect the length of life of the plants.

The removal of the nodal roots markedly reduced the number of tillers formed per plant compared with the control, particularly in the later stages of the experiment. The removal of the primary seminal root had an effect more or less intermediate between that seen in the control and the nodal amputation treatments, whereas amputation of the lateral seminal roots had an effect little different from that seen in the control. The plants receiving superphosphate tended to produce rather more tillers than those not receiving superphosphate but the difference was not significant. The herbage was cut during the 14th week of the experiment and again during the 20th week. The amputation of the lateral seminal roots did not significantly reduce the herbage yield, whilst the amputation of the primary seminal root significantly reduced the yield and the amputation of the nodal roots resulted in a still greater reduction, ending in the death of the plants so treated. The application of superphosphate increased the yield of herbage. From this experiment, Yates and Jacques concluded that the lateral seminal roots did not make any marked contribution to the food supply. The primary seminal root could keep the spring-sown seedling alive for 3·5 months from the time of sowing the seed. The nodal root system took over the function of absorption from the seminal root system, but the latter had a measurable effect on tiller and leaf production for fully 5 months (the duration of the trial) over and above that of the nodal roots.

Weaver and Zink (1945) also found that seminal roots alone were able to support plants for a considerable length of time, in some cases, four months. Seeds of *Andropogon furcatus*, *Sorghastrum nutans*, *Bouteloua gracilis* and *Panicum virgatum* were sown on 1st June and their nodal roots were removed as they were formed. The plants grew well, but some died during a period of severe conditions which promoted rapid transpiration in July. Growth continued until September, after which considerable degeneration took place, although one or two plants of each species remained alive on 1st October.

Slightly different results from those of Yates and Jacques were obtained by La Rue (1935) who amputated the seminal roots of plants of *Holcus sudanensis* and *Phalaris arundinacea* just below the seed prior to the formation of nodal roots. Nodal roots appeared on the cut plants soon after the removal of the seminal roots, long before they appeared on the control plants. The seedlings deprived of their seminal roots proved to be capable of normal growth and La Rue was of the opinion that the loss of the seminal roots was of little consequence in the survival of the plants.

Growth of the Seminal Roots

In 1939, Sinnott pointed out the suitability of certain small-seeded grass species for studies on the growing meristem of the seminal roots. Since then these species have been widely used for this purpose as the transparency of the fine roots and the rudimentary characteristics of the root caps permit unobscured microscopic observation of the surface of the living meristem.

The root cap, in such small-seeded grasses as *Agrostis*, *Poa*, *Sporobolus* and *Phleum* spp., was described by Sinnott (1939) as being composed of a few rather loose cells. Goodwin and Stepka (1945) agreed with this statement so far as *Phleum pratense* was concerned and further stated that its boundaries were clearly delineated.

Beyond the root cap, Goodwin and Stepka (1945) distinguished several zones of growth in the young roots of *Phleum pratense*. The meristematic zone, which they defined as that portion of the root in which transverse cell divisions were taking place, consisted of the apical 425μ, exclusive of the root cap. This region they sub-divided into two parts: (1) the apical 200–300μ, characterized by slow growth and the presence of 'typical' (small, richly protoplasmic, non-vacuolated) meristematic cells; and (2) the basal 125μ characterised by extremely rapid elongation and cell division, and the presence of vacuolating dividing cells. According to these workers, the growth processes in the apical portion of the meristem were probably limited by a shortage of food supplies. Even though organic materials were possibly transported by the mature sieve tubes of the proto-phloem to within 230μ of the root apex, from there they had to pass through a series of undifferentiated cells which were actively utilising such materials for their various activities. Hence, a decreasing concentration gradient would be set up with the most acute shortage at the root apex. Therefore, they did not find it surprising that the average cell size in the epidermis, and in some, if not all, of the underlying tissue was significantly larger at the

apex of the root meristem than it was further back along the axis where more frequent cell division was taking place. In the rapidly elongating portion of the meristematic zone, the rates of cell division and root elongation appeared to be many times more rapid than they were towards the tip. Here the cells were apparently well supplied with the organic materials necessary for growth by the mature sieve tubes which traversed this zone, In the basal portion of the meristematic zone, which appeared to be the principal location of root elongation, there was some increase in average cell size and a beginning of vacuolation of the protoplasts.

The zone of 'cell elongation' they considered as falling between 400 to 1000μ from the base of the root cap. In this zone the root elongated relatively slowly, and as there was little, or no, cell division this elongation was correlated with the presence of 'vacuolated extending' cells. Actually, the average length of the cells began to increase at about 300μ from the apex, well within the meristematic zone, a gradual transition from one stage to another taking place.

Sieve tubes were matured in the meristematic zone and the xylary elements were differentiated further back, frequently in the zone of cell elongation. The youngest of these elements were probably matured as a functional part of the xylary system near the point where root hairs commenced to develop and where the root became prepared to play its absorptive role. Root hairs normally developed behind the zone of elongation, otherwise they would have been sheared off as the growing portion of the root slid past soil particles.

Brumfield (1942) studied single meristematic cells and complexes resulting from their division in similar roots. He was of the opinion that each cell, or its resultant complex, passed through two phases of growth, elongation proceeding at a constant exponential rate in each. In the first phase, the cell, or complex, elongated at about 5·4% per hour. This occurred in the region from the root tip to 140μ behind it. At the end of this phase the growth-rate increased from 5·4 to 41·2% per hour, this transition taking place in the zone from 140 to 310μ behind the root tip. During the second phase the growth-rate remained constant at the figure of 41·2% per hour, falling off rapidly to zero at the end of the phase which occurred at 970μ behind the root tip. Cell division occurred only during the first phase which appeared to be primarily concerned with the production of new protoplasm while the second was concerned with vacuole enlargement.

The two growth phases postulated by Brumfield are not in agreement with the results of Goodwin and Stepka which indicated that a cell's growth-rate is constantly changing with its position in the root. This latter view is supported by the observations of Sinnott (1939) that there was a definite gradient in the rate of cell expansion, beginning just before division ceased and gradually increasing until maximum growth was attained. Goodwin and Stepka suggested that the discrepancy of views may be due, in part, to Brumfield having estimated growth-rates from cell complexes 100 to 600μ in length, whereas the total length of the most rapidly growing zone, according to their results, may actually be as short as 50μ.

The shape and position of new walls laid down by dividing cells was studied by Sinnott (1939) in the genera *Poa*, *Phleum*, *Agrostis*, *Chloris* and *Sporobolus*. He stated that the cells in all layers were in regular longitudinal rows, so that the new walls, with rare exception, were transverse or essentially so. In equational divisions the walls were straight, but in non-equational ones, as in divisions giving rise to root-hair initials in some genera, they were commonly curved from the first, with the convex side towards the larger cell. A new wall was never laid down directly opposite a previously formed cross-wall of any neighbouring cell. If the natural position would tend to bring it into such a relation this was avoided by the bending of the new wall, so that it joined the side wall at a point at one side or the other of the place where the cross-wall of the neighbouring cell was attached. The actual point where a new cross-wall joined the side wall seemed to be determined by an equilibrium between a tendency to divide the mother cell equally (or into two parts of definite proportions) and the tendency to bisect the free side-wall space.

Further work was carried out with the same genera, excepting *Agrostis*, by Sinnott and Bloch (1939b). They stated that the changes in intercellular relationships observed in this material resulted from differing rates of growth in different parts of the cell wall. The three-dimensional-shape changes in the cells of *Phleum pratense* were observed by Mozingo (1951), who found that 121 cells just before division averaged 11·26 faces, while their 200 daughter cells averaged 9·25 faces.

After growth these 200 cells, just before division, averaged 11·43 faces while their 400 daughter cells averaged 9·23 faces. Faces in certain positions and combinations were more common than others.

Brumfield (1942) was unable to find any evidence for 'rhythmic' growth, nor is there any evidence in Goodwin and Stepka's data. Similarly, neither Brumfield (1942), Cormack (1944) nor Sinnott (1939) was able to find any evidence for 'sliding' growth.

According to Goodwin and Stepka (1945), illumination had little effect upon the growth-rate of *Phleum pratense* roots. More recently, Brumfield (1953a) has reported that curvatures were induced in such roots when exposed unilaterally to ultraviolet radiation. Low doses induced a curvature away from the source of light while higher doses induced two curvatures, one towards the source, which occurred in the basal part of the growing point soon after exposure, and one away from the source, which occurred later, and closer to the root apex. The division of the surface cells was inhibited but elongation continued at a reduced rate, resulting in the affected cells becoming enormously long; in some cases they were unable to keep pace with the growth of the unaffected cortical cells beneath, resulting in the separation of end walls of adjacent surface cells. (Brumfield, 1953b). Pre-treatment with indoleacetic acid did not materially affect the curvatures induced by ultra-violet irradiation (192,000 ergs/cm.^{2}, 2537Å), whereas the curvatures toward and away from the source were completely inhibited by pre-treatment with 10 mg./l. of 2,4,6-trichlorophenoxyacetic acid (Brumfield, 1955).

The incorporation of coumarin and scopoletin into the growth media has been shown to inhibit the growth of the seminal roots of *Phleum pratense*, coumarin being about fifty times as effective as scopoletin. Coumarin appeared to upset the polarity of growth, particularly in the region of cell elongation, but did not eliminate meristematic activity or root-hair development. Scopoletin seemed to inhibit the whole growth process (Pollock, Goodwin and Greene, 1954).

Positive geotrophic curvatures may be induced in seminal roots when they are placed horizontally. In *Lolium italicum*, this response has been shown to be abolished by pre-treatment of the roots with certain analogues and derivatives of 2-benzol-benzoic acid (Jones, Metcalfe and Sexton, 1954). Pre-treatment with indoleacetic acid markedly reduced the growth of the seminal roots of *Phleum pratense*, but did not materially affect the amount of curvature per unit of growth. Pre-treatment with 2,4,6-trichlorophenoxyacetic acid solution did not effect growth, but the geotrophic response was greatly modified, no response being observed in roots treated with 50 mg./l. (Brumfield, 1953).

CHAPTER 2

NODAL ROOTS

Nodal roots are also called adventitious, crown and secondary roots. They are of small diameter, fibrous and greatly branched, ramifying throughout the upper region of the soil; their tensile strength and resistance to injury is considerable, so much so that the roots of certain grass species are employed as bristles in heavy brushes (Ercilla, 1952). They are produced after the seminal roots, and, with rare exceptions, arise endogenously from the stelar tissue of nodes on the stem (Goossens, 1936), either a true stem, a rhizome or a stolon (Arber, 1934).

The nodal roots of *Agropyron cristatum*, *A. pauciflorum* and *Bromus inermis* were reported by Pavlychenko (1942) to differ from the seminal roots in that they possessed swollen bases, whereas the seminal roots were of the same diameter from base to root tip. More nodal roots were produced than seminal roots and Pavlychenko was of the opinion that the number of seminal roots was largely a genetic character, while the number of nodal roots depended largely upon the environment. Villares, Tundsi and Becker (1953) did not mention swollen bases when describing the nodal roots of *Panicum maximum* but stated that they tapered almost imperceptibly from the point of junction with the rhizome to their apex. In British Somaliland, Glover (1951) noted that the root tips of certain species (*Eragrostis hararensis* and *Panicum turgidum*) were swollen.

The position between the seed and the soil surface at which the lowest, or first, node forms, i.e. the first position at which a nodal root can be initiated, is controlled, according to Zijlstra (1939), by the elongation of the mesocotyl and the epicotyl. The mesocotyl is a segment inserted between the cotyledon sucker and the coleoptile, while the epicotyl is an inferior stem segment occurring between the origin of the coleoptile and the first node (Fig. 1). Zijlstra distinguished between plants in which the epicotyl elongates more than the mesocotyl, and vice versa. Other workers (Evans, M. W., 1927; Arber, 1934) have only mentioned the elongation of the mesocotyl. Evans, M. W., (1927) stated that the nodal root system of *Phleum pratense* tended to become established near the soil surface, irrespective of the depth of planting, the adjustment taking place through variations in the length of the mesocotyl, which could elongate to a maximum of 0·91 in. Arber (1934) suggested that the adjustment in the length of the mesocotyl was controlled by light, a lack of it causing elongation. Roots rarely develop from the mesocotyl, though short appendages resembling root hairs commonly develop from it. These 'root hairs' were noted by Nishimura (1922) on plants of *Phleum pratense* and *Poa pratensis* and by Schwartz (cited by Haberlandt, 1914) on *Panicum miliaceum* and *Setaria italica*. The production, by *Festuca rubra*, of a small number of roots at the base of the mesocotyl was observed by Howarth (1927) who stated that they were nodal roots, not cauline such as have been found in a similar position in *Avena* sp.

The normal plan of initiation of nodal roots by *Bouteloua curtipendula*, according to Olmsted (1941), involved the differentiation of one primordium at the coleoptilar, or second, node at the level of the insertion of the coleoptile, and on the same side of the axis and in the same plane as the line along which the coleoptile splits. Successive nodes up to the first or second below the first 'elongating' internode normally produced a pair of primordia on the side of the axis opposite the bud insertion at the same node. The actual number of primordia produced by the primary axis, however, rarely agreed with this 'normal' plan as two tendencies appeared to be imposed upon this 'normal' development. Firstly, the number of primordia at a node appeared to vary directly with the amount of water available in the soil and secondly the number of primordia initiated at the higher nodes and on secondary axes, i.e. in the later stages of growth, in individual plants varied inversely with the number of primordia on other nodes which had previously matured into functional roots. The first nodal root of *Buchloë dactyloides* was stated by Webb (1941) to appear directly below the first tiller of the crown node, starting to grow 10 days after the seed was sown and when the seminal root had attained approximately one-third of its full length. This first root grew at a rate of 1 cm. per day, and, when it had attained a length of 2 cm., another nodal root originated from a second tiller which had been produced. These main roots sent out branch roots

at 0·5 cm. intervals and continued to grow throughout the growing season. Each tiller of a grass plant is capable of forming its own root system (Mitchell and Coles, 1955) and to some extent at least, each tiller acts as an independent unit (Crider, 1955) (p. 95).

Olmsted (1941, 1942) stated that three consecutive days of surface wetness were required by the nodal roots of *Bouteloua curtipendula* to allow them to penetrate sufficiently to become established, and that, unless a seedling established nodal roots before a period of drought, it was unlikely that it would survive. In established plants, drought, when it prevented the establishment of nodal roots, tended to stimulate the initiation of root primordia. Under extreme moisture deficiency, however, Glendening (1941) found that the initiation of nodal roots by seedlings of *Heteropogon contortus* was seriously curtailed. Pavlychenko (1942) noted that a greater number of nodal roots were formed by seedlings of three perennial species when receiving irrigation, than when grown under arid conditions, and Weaver and Zink (1945) found that nodal root production in several grasses was promoted when the surface soil was consistently moist and the humidity favourable for growth.

Recently initiated roots of *Lolium perenne*, *Lolium italicum* and *Festuca arundinacea* were described by Schwass and Jacques (in press) as being white in colour. This whiteness lasted approximately 6 to 9 weeks after which lateral branches were formed, the zone of root hairs became restricted and the colour darkened to cream. As the roots aged the colour further darkened to brown. The white roots rarely reached more than eight inches in length and they contained less dry matter than darker-coloured roots.

The addition to the growth media of plant hormones has been found to stimulate the production of roots from the cuttings of many species. In tests with indole- and naphthyl-acetic acids in several concentrations and media, Nowosad (1939) found that the only positive response *Phleum pratense* gave was to 100 ppm. naphthyl-acetic acid on charcoal. The response to this treatment was not considered to be sufficient to justify its practical use.

The treatment of plants of *Sorghum halepense* with a solution of the diethanolamine salt of maleic hydrazide was stated by Levi (1955) to result in the formation of a crown of adventitious roots on the first node of plants especially if they were defoliated after the treatment with the salt solution. No such roots were formed on any of the untreated plants. Occasionally roots were initiated on the second nodes as well. Additional roots were not noted on plants of *Paspalum dilatatum* and *Paspalum distichum* receiving similar treatment.

Certain investigators have pointed out a significant relationship, in species other than herbage grasses, between the production of Vitamin B_1 (thiamin) in the green leaves of growing plants and its translocation to the roots, where it produced a marked stimulating effect on root elongation. Ahlgren, G. H. (1941), working with young plants of *Poa pratensis*, *Poa trivialis* and *Agrostis tenuis* growing in sand culture, was unable to detect any difference in the root- and shoot-growth of plants receiving Vitamin B_1 from those not receiving it.

The process of decay in a root apparently starts in the cortex and later spreads to the stele. Goedewaagen (1955 personal communication) has described decay in temperate grasses as commencing with the sloughing off of the cortex from the stele in the older parts of the root, a process which gradually extends to the younger parts. Schwass and Jacques (in press) working with *Lolium italicum*, *L. perenne* and *Festuca arundinacea* in New Zealand stated that the cortex of the roots of plants produced from seed sown in the late winter became soft to finger pressure in early summer and a loss of cortex occurred in late summer. Many roots showed a complete loss of cortex over several inches proximal to the crown of the plant. These roots were still attached to the plants when their observations ceased the next spring. As a result of experiments employing the 'bleeding' technique (p. 133), Goedewaagen was of the opinion that the bare stele was capable of transporting water and nutrients from the region of absorption i.e. the root tip and to a lesser extent that part of the root which retained its cortex, to the aerial parts of the plant.

Some confirmation of these morphological observations is forthcoming from the work of Schwass and Jacques using 2, 3, 5-triphenyl tetrazolium bromide as a vital stain, the intensity of colour produced by this compound indicating the degree of biological activity. The root cap was found to stain most intensely while the cortex of young white roots stained less strongly; the stele of these roots could not be examined because of

the opaqueness of the cortex. The cortex of older roots did not stain, or did so only to a slight degree, while the stele stained strongly as did the steles of portions of roots from which the cortex had sloughed off. These results would appear to indicate a gradual lessening of biological activity in the cortex as it becomes older until it sloughs off from the stele; the stele remains active even after the cortex has disappeared. It would appear that the roots of these species (*Lolium perenne*, *L. italicum* and *Festuca arundinacea*) have an early deciduous cortex (p. 16).

Polymorphism

The occurrence of more than one type of nodal root on a single plant has been reported for several species. A distinction between long unbranched roots and shorter branched roots has been noted in *Phalaris arundinacea* (Arber, 1934), *Spartina townsendii* (Oliver, 1925), *Phleum pratense* (Evans, M. W., 1927), *Lolium perenne* (Jacques, 1937a; Roberts and Hunt, 1936), and *Cynosurus cristatus* (Jacques, 1937a). Oliver called the long unbranched roots of *Spartina townsendii* anchoring roots and the branched ones nutritive roots, according to their supposed functions. The anchoring roots arose from the base of the stocks, where the green shoots were attached, and from the joints of the rhizomes. While these anchoring roots were mainly unbranched, some, which were inserted rather higher up the stock, carried lateral roots on the proximal 2 inches; the distal parts descended unbranched. The nutritive roots formed a dense plexus in the upper few inches of the mud in which the plants were growing. They were of limited extension and were inserted at a slightly higher level on the stocks than the anchoring roots, and grew in all directions. There were also roots which were transitional between the extreme types.

Jacques (1937a) described three types of nodal root formed by *Lolium perenne* and *Cynosurus cristatus*. These were:—

(i) The 'white' roots which were thick, glossy, straight, and, during early development, unbranched; after a time they became profusely branched. Before branching occurred the whole surface was covered with root hairs, but, after branching started, root hairs developed behind the growing points of the branched roots only and did not extend for any great distance along the root.

(ii) The truly 'fibrous' roots, which differed from (i) at the outset in that they were of a smaller diameter, were wavy and became fibrous at an earlier date. Their root hairs were apparent immediately behind the points of elongation only.

(iii) A type which appeared to combine some of the characters of both (i) and (ii), except that their root hairs were as in (ii).

This description thus agrees in many details with that of Oliver's. Both workers described two major root types and an intermediate type, the main differences apparently being that Jacques stated that the thick roots do branch in the later stages of development, a point which was not mentioned by Oliver.

The roots of *Dactylis glomerata* were classified by Kokkonen (1931b), using a similar system to that of Oliver's, except that the intermediate roots were placed by Kokkonen in a separate category. Kokkonen based his classification upon work carried out on cereals in which the function, period of development, structure and position of the roots were studied. In the cereals, the major difference between anchoring (prop) and nutritive (nutrition) roots was that in the latter the total area of the vessels in transverse section increased with the distance from the neck of the root, even although the number of vessels decreased, whilst in the anchoring roots this area decreased. The outer layers of the cortex of the anchoring roots were lignified for comparatively great lengths (4–7 cm.), thus stiffening the root. The anchoring roots were found nearest the soil surface, the anchoring-nutritive roots were somewhat deeper and the nutritive roots deeper still (Kokkonen, 1931a).

Dimorphism of a slightly different kind has been described in *Bromus inermis* by Cook (1943). One type of root was slightly larger in diameter than the other, was of a lighter colour and was produced only from tillers and rhizomes. The second type was smaller in diameter, darker in colour and more extensively clothed in root hairs. This latter type arose from the sub-crown internode and from the first crown-node, making up the major portion of the plant's root system. The 'small' roots penetrated to a depth of 2 to 3 times that of the 'large' roots and produced a dense network of fine branches.

The production of the various types of roots has been correlated in *Lolium* spp. with the environment. Rappaport (1938), working with *Lolium perenne* found that long, coarse, unbranched roots were produced in water culture and shorter, finer, branched roots in soil. Only one type of root was produced by a plant when all the roots were in one medium, but both types were produced by a single plant when part of its root system was in water and part of it in soil. Working with plants of *Lolium* spp. grown in soil, Mitchell (1954) found that plants under poor environmental conditions (700 foot-candles light intensity and 65°F.) had wavy, fibrous roots only, while those grown under environmental conditions favourable to growth (2000 foot-candles and 50°F.) had a root system composed mainly of thick, glossy, white, straight roots, similar to those described by Jacques (1937a), with only a few fibrous roots. In an intermediate environment of 700 foot-candles and 50°F. the roots were a little more robust than at 700 foot-candles and 65°F., but no white roots were present. At 2000 foot-candles and 65°F., white roots were present, but in a smaller proportion than at 2000 foot-candles and 50°F. (p. 89).

Branching

Most main nodal roots exhibit a high degree of branching, branches of the third order commonly being produced (Table 1). Considerable variation occurs between species in their degree of branching (Table 2). Competition from other plants reduces the amount of branching displayed by a plant's root system (Pavlychenko (1942), see p. 116).

Jefferies (1916) termed the main roots of *Molinia caerulea* 'cord' roots, and their branches, 'fibrous' roots. The cord roots were 1·5–2·0 mm. in diameter and descended 15–45 cm. They retained their thickness throughout most of their length, tapering very slightly to within 3 cm. of the tip, after which they tapered rapidly to terminate in a blunt root-cap. Close to the rhizomes they squeezed each other out of shape. The fibrous roots were 0·3–0·8 mm. in diameter and 13–35 cm. long and they branched freely in all directions. Both types of root showed the same general anatomical structure. A similar dimorphism was described by Barley (1953) in *Phalaris tuberosa* and *Paspalum dilatatum* and to a lesser extent in *Lolium perenne* and *Dactylis glomerata*. Barley described the main roots as being of wide diameter and penetrating more or less vertically, and the lateral roots as being of lesser diameter, fibrous, and obliquely ramified.

The diameter and tensile strength of roots has been shown by Pavlychenko (1942) to decline progressively from the main roots to the lowest order of branches (p. 12). According to Rappaport (1938), in young spaced plants of *Lolium perenne* most of the branches occurred in a lower layer of the soil than did most of the main roots. (Table 18).

Pavlychenko (1942) stated that the branches, unlike the main roots, of the plants he studied were composed of young actively absorbing tissue and that the ability of a species to compete with associated plants and its value for the reclamation of 'worn-out' lands depended upon the number of its branches. Dittmer (1938) working with *Poa pratensis* found more and longer root hairs per unit length on the main roots than on their branches, so that the root hairs of the main roots had a considerably greater surface area than those of the branches.

Tensile Strength

The diameter and tensile strength of the main roots and their branches of 11 species of grasses were measured by Pavlychenko (1942) (Table 3).

TABLE 1

Quantitative analysis of the roots of *Poa pratensis*.
Values given are the average for three soil samples each 3″ in diameter × 6″ deep (42 cubic inches)
(*Dittmer*, 1938)

Root categories	Total no. of roots	Av. root length (mm.)	Total length of roots (ft.)	Av. diameter of roots (microns.)	Total root surface (sq. in.)	Volume (cubic mm.)
Main	900	64·0	180	480	134	9,750
Secondary	39,700	6·6	870	135	173	3,800
Tertiary	43,900	1·4	200	85	25	350
Totals	84,500		1,250		332	13,900

TABLE 2

Quantity of underground parts of certain grasses grown in swards found in the upper 10 cm. of soil per area of one half-square metre (*Pavlychenko*, 1942)

	Agropyron smithii	*Andropogon furcatus*	*Andropogon scoparius*	*Bouteloua gracilis*	*Poa pratensis*	*Sporobolus cryptandrus*	*Stipa spartea*	*Agropyron cristatum*	*Agropyron pauciflorum*	*Bromus inermis*
Underground stems										
Length (m.)	104·6	19·8	16·0	7·6	27·7	9·1	11·5	23·4	4·5	41·1
Weight of dry matter (g.)	58·2	154·0	97·8	39·0	108·6	43·0	39·0	153·6	41·9	125·5
No. of buds per crown							3–57	12–23	3–8	6–17
" " " per cm. of rhizome	0·1	0·6	0·8		0·05	1·3				0·3
Main roots										
Number	11,528·0	3,472·0	3,397·0	5,829·0	16,278·0	4,372·0	4,378·0	11,688·0	8,070·0	11,410·0
Length (m.)	1,037·5	277·8	305·7	408·0	1,139·5	481·1	44,446·0	935·3	562·8	1,026·2
Weight of dry matter (g.)	34·8	76·4	36·0	29·6	67·2	68·4	46·0	58·4	31·8	60·8
Branches 1st Order										
Number	630,961·0	108,600·0	244,584·0	489,600·0	1,937,000·0	1,049,280·0	109,647·0	654,000·0	529,739·0	617,317·0
Length (m.)	43,534·3	4,722·9	11,006·3	9,781·6	75,480·0	13,733·5	6,384·5	39,240·0	21,179·6	37,039·1
Branches 2nd Order										
Number	1,652,294·0	543,000·0	3,301,884·0	4,798,400·0	10,567,000·0	3,774,700·0	1,196,151·0	7,852,700·0	2,279,250·0	2,850,000·0
Length (m.)	52,873·4	11,614·0	16,493·5	10,090·0	95,084·4	16,498·6	8,373·1	54,968·9	15,955·0	9,500·0
Branches 3rd Order										
Number	3,721,138·0	2,267,600·0	4,952,626·0				1,509,905·0	3,135,300·0	1,149,230·0	
Length (m.)	7,442·3	4,535·2	9,904·3				3,019·8	9,466·5	3,102·9	
All branches										
Number	6,004,393·0	2,919,200·0	8,499,094·0	5,288,000·0	12,564,000·0	4,823,980·0	2,815,703·0	11,642,000·0	3,958,219·0	3,467,317·0
Length (m.)	103,850·0	20,872·1	37,404·1	19,871·6	170,564·4	30,232·2	17,777·4	103,675·4	40,237·4	46,539·1
Weight (g.)	52·2	114·6	54·0	44·4	101·0	102·6	69·0	87·8	47·7	91·5
Total										
Length (m.)	104,992·1	21,169·7	37,725·8	20,287·2	171,731·6	30,722·3	18,234·9	104,634·1	40,804·8	47,607·1
Weight of dry matter (g.)	145·2	345·0	187·8	123·0	276·8	214·0	154·0	299·8	121·4	277·8

TABLE 3

Diameter and tensile strength of grass roots

(*Pavlychenko*, 1942)

Species	Base of culm		Rhizome		Main root		Branches of 1st order		Branches of 2nd order		Branches of 3rd order	
	Diam. (mm.)	Tensile strength (g.)	Diam. (mm.)	Tensile strength (g.)	Diam. (mm.)	Tensile strength (g.)	Diam. (mm.)	Tensile strength (g.)	Diam. (mm.)	Tensile strength (g.)	Diam. (mm.)	Tensile strength (g.)
Agropyron smithii	2		2·1	2882	0·46	849	0·18	79·4	0·03	2·0	0·018	0·8
Andropogon furcatus	3·4		4·1	3129	1·1	1712	0·23	623·0	0·11	64·0	0·05	2·0
Andropogon scoparius	2·4		2·2	5678	0·41	1171	0·1	31·0	0·06	6·0	0·02	2·0
Bouteloua gracilis	1·2		1·8		0·31	757	0·06	71·6	0·02	7·0		
Poa pratensis	1·4		1·3	1864	0·19	273	0·04	9·7	0·018	1·2		
Sporobolus cryptandrus	2·1		1·9	568	0·62	821	0·07	17·0	0·02	2·9	0·006	1·5
Stipa spartea	1·7	712			0·66	981	0·21	294·9	0·09	26·0	0·028	4·0
Agropyron cristatum	1·4	1002			0·4	821	0·09	88·0	0·04	8·0	0·01	1·3
Agropyron pauciflorum	1·6	583			0·5	389	0·1	19·0	0·03	1·6	0·007	0·5
Bromus inermis	1·8		1·5	2737	0·6	651	0·1	30·5	0·04	6·4		

The tensile strength of the underground stems, main roots and their branches varied within a species, and much more so between the same structures in unrelated species. Tensile strength was in no way correlated with differences in diameter of roots of unrelated species but increased directly with the diameter within the same species. Stevenson and White (1941) also determined the diameter and tensile strength of the roots of three of the species investigated by Pavlychenko. Their results for tensile strengths were somewhat lower than those of Pavlychenko in the case of the main roots, but the root diameters were also somewhat smaller so that the tensile strengths per unit diameter were, in two cases (*Bromus inermis* and *Agropyron pauciflorum*), approximately higher than, and in one species (*Agropyron cristatum*) the same as, those of Pavlychenko. The species were in the same order of merit with regard to tensile strength and tensile strength per unit diameter in both investigations, but not with regard to root diameter. Some of the differences between the two investigations may be due to the fact that Stevenson and White used living roots while Pavlychenko used roots which had been preserved in 4% formaldehyde solution. Little information is given on the age of the roots used in these investigations; variable results would be expected if some roots were older than others, especially if some of them had lost their cortices by decay.

Crider (1945) measured the diameter and tensile strength of the roots of nine-week-old plants of twelve species. Generally the species with roots of large diameter also had roots of high tensile strength. Of the species measured *Eragrostis curvula* had the greatest diameter (0·044 in.) and the greatest tensile strength (2·43 lb.).

Prior to these investigations, Kirk, Stevenson and Clarke (1937) had noted that the roots of *Agropyron cristatum* were stronger than those of *Agropyron pauciflorum*. More recently, Barley (1953) found that the main roots of *Paspalum dilatatum* had a higher tensile strength than those of *Phalaris tuberosa*, although the latter had a larger diameter.

Mycorrhiza

The presence of mycorrhiza has been reported in the roots of numerous species of grasses (Jefferies, 1916; Peyronel, 1922, 1923–4; Heath and Luckwill, 1938; McLennan, 1926; Samuel, 1926; Mason, 1928; Rayner, 1927; Asai, 1934; Kelley, 1950; Dominik, 1951; Truszkowska, 1951; Winter, 1953; Nicolson, 1955). All these mycorrhiza were apparently endotrophic.

Working in Great Britain with several native species, Nicolson (1955) found that the most widespread organisms infecting grass roots were endophytes of the vesicular-arbuscular type. The endophytes were present in three phases, consisting of the internal mycelium, the external mycelium and the penetration hyphae. The relative abundance of these phases varied in root samples from different habitats and communities. The internal hyphae formed characteristic vesicles and arbuscules. The hyphae of the external phase consisted of two more or less distinct elements: thick-walled aseptate hyphae and thin-walled hyphae which often became regularly septate. The thick-walled hyphae formed the permanent basis of the external mycelium, and the thin-walled hyphae mainly performed temporary rhizoidal and penetration functions. External

vesicles were sometimes protected by a rudimentary hyphal sheath, and in some cases the vesicles formed aggregates resembling fruiting bodies. Saprophytic development of external mycelium occurred under certain conditions. The endophytes could possibly effect a transfer of substances from soil to root when abundant external mycelium and numerous penetrations were present.

The exact significance of these associations does not seem to be known (Rayner, 1927; Winter, 1953). Brown, R. (1933) suggested that the mycorrhiza of *Lolium* was capable of fixing atmospheric nitrogen, but this was doubted by Harley (1950). McLennan (1926) provided evidence that the fungus she studied in the roots of *Lolium* formed fat which was ultimately discharged into the cells of the root, where it was presumably hydrolysed, before being translocated during the fruiting season of the host.

Rhizosphere

The subject of soil micro-organisms and the rhizosphere was reviewed by Katznelson, Lochhead and Timonin (1948) but the literature directly dealing with herbage grasses is very small. Wallace and Lochhead (1949) were of the opinion that the type of bacteria in the rhizosphere varied with the plant species, a view held by many other workers. Wallace and Lochhead divided the species they were working with into two groups differentiated by the species of bacteria in their rhizospheres; the first group consisted of *Trifolium pratense*, *Medicago sativa*, and *Linum usitatissimum*, and the second group of cultivated *Triticum*, cultivated *Avena* and *Phleum pratense*.

More detailed work on *Phleum pratense* plants has been reported from Russia by Fedorov and Nepomiluev (1954). They stated that when the plants were growing vegetatively the chief rhizosphere bacteria were fluorescing and denitrifying but when the flower stalks were emerging myco-bacteria were the most numerous. The rhizosphere population was greatest at the flowering stage and decreased sharply in the spring and autumn. The size of the population was less in the third than in the second year of life of the plants. The population was the same in pots as in the field and in pot experiments organic and mineral fertilizers increased the number of bacteria in the rhizospheres.

In Finland, Gyllenberg (1955) investigated the rhizosphere effect of four grasses, *Phleum pratense*, *Poa pratensis*, *Anthoxanthum odoratum* and *Deschampsia flexuosa*, in virgin soils. It was found that the number of bacteria was eleven to thirty-one times higher in the rhizosphere of these plants than in the corresponding non-rhizosphere control soils. The effect on non-sporogenous bacteria seemed to be constant since it was independent of the plant species, the stage of plant development and the soil conditions. The promoting effect on spore-forming bacteria and actinomycetes varied with different plants and showed dependence on the stage of plant development and the soil conditions. The major part of the sporogenous strains which were isolated were related to *Bacillus cereus*. This type predominated in the rhizosphere samples, but in the control samples types related to *Bacillus pantothenicus* were also found. Among the non-sporogenous isolates gram-negative types were somewhat more abundant than gram-positive types. The gram-negative strains obviously belonged to the genera *Pseudomonas*, *Achromobacter*, and *Flavobacterium* and the gram-positive to the *Corynebacterium*.

CHAPTER 3

ANATOMY OF NODAL ROOTS

In general, the anatomy of a grass root resembles that of a 'typical' monocotyledon, the tissues of a mature root in transverse section, working towards the centre being: epidermis, exodermis, sclerenchyma, parenchyma, endodermis, stele (consisting of pericycle, phloem and xylem bundles together with ground tissue) (Fig. 2).

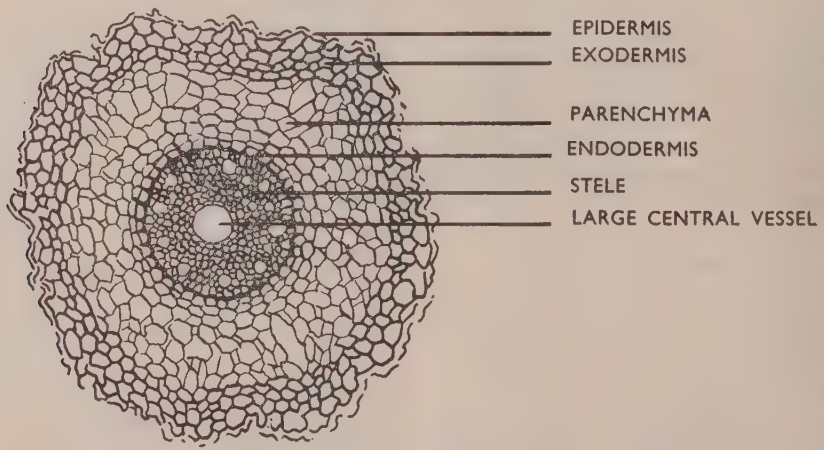


Fig. 2. Transverse section of a nodal root of *Festuca pratensis* showing details of the cortex. (*Drawn from a photograph by P. Turner of the Grassland Research Institute, Hurley, England*)

The differentiation of the cortical tissues in South African grasses was studied by Goossens (1936) who found that the epidermis and exodermis were formed from the two outermost layers of primary cells. The succeeding layer of primary cells divided by means of oblique walls to form sclerenchymatous tissue. In roots with a soft deciduous cortex this layer of sclerenchyma consisted of one row of cells only, while in those with a hard persistent cortex 2 to 5 or more rows were formed by irregular division in the region of maximum thickness. From the remaining layers of primary cells the parenchyma, which retained a more or less radial placement, was formed. The endodermis developed from the innermost layer of primary cells and remained one layer thick.

The epidermis of *Molinia caerulea* was described by Jefferies (1916) as consisting of medium-sized, thin-walled cells with no cuticle and with a longitudinal section 4 to 8 times their diameter. This layer was supported by one or two layers of similar cells. The absence of the cuticle suggested that the roots themselves function as absorbing organs. In South African grasses, Goossens (1936) stated that the epidermal cells varied little in shape and size; their outer tangential walls were always arched outwards and they fitted closely against the next layer of cells. The layer of cells immediately below the epidermis was usually clearly marked off from the surrounding tissue and Goossens considered that it corresponded to the exodermis which is found in most other monocotyledons. This layer of cells presumably corresponds to Jefferies' 'supporting' cells. When first developed, the cells of the exodermis were all of the same size, but when elongation took place some remained shorter than others. In the early stages the cells had thin cellulose walls, but, as they aged the walls thickened, a suberin lamella being formed which was often followed by a tertiary lamella of cellulose impregnated with lignin. In species with an early deciduous cortex the cellulose was poorly developed. All the walls of the short or 'passage' cells, except the outer tangential ones, remained unthickened.

The layer of sclerenchyma in *Molinia caerulea* was described by Jefferies as consisting of several rows, usually three, of narrow fibres; their walls were thickened with cellulose which later became lignified. These fibres were 800μ long, roughly three times the length of the neighbouring elements. In South African grasses the degree of development of this layer varied with the persistency of the cortex (Goossens, 1936).

The cortical parenchyma of *Molinia caerulea* was divided by Jefferies (1916) into three zones:—

Outer zone. Cells of varied size and shape, irregularly arranged, their size increasing with distance from the sclerenchyma.

Middle zone. Cells practically circular in transverse section and gradually assuming an arrangement of radial rows separated by air spaces. The air spaces were of schizogenic origin and died out at the inner margin of the zone.

Inner zone. Perfect radial arrangement of cells, rows very closely applied to one another. The individual cells becoming smaller and rectangular as the endodermis was approached.

The cells all had thick walls with prominent pits. The outer and middle zones usually contained starch grains and these, together with the cellulose walls, were considered by Jefferies to be food reserves. (Page 49 *et seq.*). In South African grasses this tissue was described by Goossens (1936) as being characterised by isodiametric radially placed cells. The walls of the young cells were composed of cellulose which soon became lignified; Jefferies mentioned cellulose only. Newly-formed cells contained much protoplasm which generally decreased as the cells aged. All layers of cells, except those bounding the endodermis, i.e. those corresponding to Jefferies' inner zone, were broken up by the formation of inter-cellular spaces. These inter-cellular spaces, which were considered by both Jefferies and Goossens to be concerned with aeration, were found by Goossens to vary in size with the soil moisture and the time of the year when the roots were developing. High soil-moisture content and summer weather both favoured the development of large spaces.

Both Klinge (1879) and Schröder (1952) were of the opinion that the anatomical structure of the roots of a species is relatively constant and both have used the appearance of the cortical parenchyma to differentiate the species they studied into major categories. Klinge's first group consisted of those species with roots having an irregular order of the cortical cells; his second group he described as having a regular disposition of cortical cells. The first group of Schröder consisted of those species with large inter-cellular air spaces arranged like the spokes of a cart wheel in the cortex; his second group consisted of those with cortical cells arranged in regular radial rows with small irregular air spaces. There is a considerable degree of similarity in the classifications of these two workers, especially in the description of the second group. Of the fifteen species studied by both, five (*Molinia caerulea*, *Nardus stricta*, *Glyceria fluitans*, *Aira caespitosa*, and *Phleum pratense*) occurred in the first group of both classifications and five (*Calamagrostis lanceolata*, *Dactylis glomerata*, *Holcus lanatus*, *Bromus mollis*, and *Anthoxanthum odoratum*) in the second. Four of the fifteen species were stated by Schröder to occur in both groups of his classification. In only one case, that of *Poa pratensis*, does a species occur in the first group of one classification and the second of the other.

The cells of the endodermis of *Molinia caerulea* were described by Jefferies (1916) as being as broad as they were deep in transverse section. Each cell was the first one of a radial row of parenchymatous cells. The outer wall, in transverse section, was thin and straight in contrast to the inner wall which was almost semi-circular, often being thickened in the middle to three-quarters of the depth of the entire cell. This wall was pierced by a series of fine pits, presumably to allow the passage of liquids from the cortex to the vascular tissue. The thickening of these walls in South African grasses was described by Goossens (1936) in great detail. While the cells were increasing in length their walls were composed of cellulose, but, on reaching full size, a secondary suberin lamella was formed. Almost simultaneously a tertiary lamella developed, consisting of cellulose impregnated with lignin. Great differences were observed in the thickness of the tertiary lamella but it remained remarkably constant in each genus. Both long and short cells occurred in this tissue, which apparently had the function of protecting the stele. In some species of *Andropogon*, Borissow (1924) found certain bodies, which he interpreted as siliceous cystoliths,

embedded in the thickening of the walls of the endodermal cells. In section these thickenings resembled screws attaching the endodermis to the central cylinder.

The differences in the structure of 'early deciduous' and 'persistent' cortices has been mentioned previously (p. 14). A persistent cortex is one which persists during the whole life of the root and decays just prior to or at the same time as the stele. An early deciduous cortex decays early in the life of the root, leaving a bare stele surrounded by the endodermis (see p. 8). Klinge (1879) was of the opinion that the mode of decay of the cortex was more or less constant within a species and used this for classification. Of the sixty-six species studied, five grasses and two cereals (*Holcus lanatus*, *Anthoxanthum odoratum*, *Avena sativa*, *Avena pratensis*, *Melica altissima*, *Hordeum vulgare* and *Leptochloa arabica*) had persistent cortices, all these species having irregularly arranged cells in the cortex (see p. 15). The amount of sclerenchyma in the roots with persistent cortices apparently varied considerably. Goossens and Stapleberg (1933) and Goossens (1936) in South Africa found that the persistency of the cortex was constant within a species, which is in agreement with Klinge, and that the species with persistent cortices were confined to moist habitats and had large parenchymatous inter-cellular spaces and well developed sclerenchyma; this latter is not entirely in agreement with Klinge. Those species with a deciduous cortex were confined to arid or dry regions and had poorly developed sclerenchyma and intercellular spaces.

In the arid regions of South Africa, Henrici (1929) noted that in the roots of certain species, especially of *Eragrostis*, the cortex was not solid, but consisted of loose threads of disintegrated or whole cells. Large cavities taking up as much as four-fifths of the root were formed. Such roots rarely branched and at certain times of the year bore abundant root hairs. Other species e.g. *Anthephora pubescens* and *Themeda triandra* only produced this type of root when the moisture was present in the soil in greater quantities than normal. When the soil moisture decreased to normal such roots lost their cortices, so becoming corky roots, which were the only type of roots seen on the plants of certain species e.g. *Digitaria eriantha*. These corky roots were without root hairs, but with abundant fine rootlets. The central cylinder occupied up to four fifths of the diameter of the whole root. It would seem possible that these roots with a loose cortex correspond to the persistent cortices of Klinge and Goossens and Stapleberg, but that the persistence of the cortex may depend upon the environmental conditions. Klinge classified the species with an irregular order of cells in the cortex into those which had a persistent entire cortex, those in which the whole cortex decayed and intermediary forms between these two extremes.

The stele does not differ greatly from those of other monocotyledons. That of *Molinia caerulea* has been described in some detail by Jefferies (1916). It was enclosed by a pericycle of small, very thick-walled, pitted cells which formed a ring made irregular in outline by the convex surfaces of the endodermal cells to which they were applied. Within the pericycle was a polyarch ring of alternating phloem and xylem bundles. The phloem bundles consisted of thin-walled sieve tubes and companion cells which were very irregular and varied in outline. On the outside of these bundles was the protophloem, the cells of which were smaller than the later-developed elements and were frequently compressed. The groups of xylem had their protoxylem adjacent to the pericycle and their large vessels adjacent to the inside. The protoxylem was composed of narrow annular and spiral vessels while the xylem proper was composed of tracheids, large vessels and xylem parenchyma. The vessels were large and distributed singly; they were almost circular in transverse outline with abundant conspicuous pits, and each was surrounded by a layer of flat parenchymatous cells. Usually vessels were developed in alternate bundles only; the other bundles remained inconspicuous through the absence of large vessels. The xylem parenchyma had its walls slightly thickened, although in comparison with the other elements, the phloem excepted, it was thin-walled. The whole of the central portion of the stele within the ring of large vessels was occupied by a sclerenchymatous tissue composed of thick-walled, long fibres with fine pits and ends rather bluntly pointed for such a tissue. Towards the centre these elements increased in sectional area but there was no thinning of the walls. The middle lamellae of the cell walls were very prominent and gave rise to strongly marked polygonal outlines. This almost solid central cylinder, whose diameter was one-quarter of the

whole, was responsible for the root having a great tensile strength.

The form of the xylem is, according to Klinge (1879), more or less constant within most species and the sixty-six species studied by him were divided into two major groups, those whose pericycle was interrupted by small xylem vessels and those whose pericycle was not so interrupted. Twenty of the species never had their pericycles interrupted; most of the Western European species were not in this class. More recently Goedewaagen (1955, personal communication) has studied the problem and found that the pericycles of *Poa pratensis* were interrupted by xylem vessels while those of *Dactylis glomerata* were not. This is in accordance with Klinge's classification. Goedewaagen was of the opinion that the interruption of the pericycle by small xylem vessels was a general phenomenon to be found in most of the grasses of the Netherlands.

Kokkonen (1931a and b) stated that in *Dactylis glomerata* the total area in transverse section of the vessels in the central cylinder of the 'nutrition' roots (see p. 9) became greater from the base to the tip while in the 'anchoring' roots this area decreased. In both types of roots the number of vessels diminished with the distance from the base. Kokkonen was of the opinion that growing 'anchoring' roots received water from the plant, not from the soil as did the other roots.

The anatomy of a root may be modified by environmental factors. The effect of soil water and season upon the development of the inter-cellular spaces in the cortical parenchyma has already been mentioned (p. 15). Defoliation of plants in most species results in the development of roots of reduced diameter, both the cortex and stele being affected, and also in a reduction in the number and diameter of the xylem vessels and phloem tubes. These reductions were shown to take place

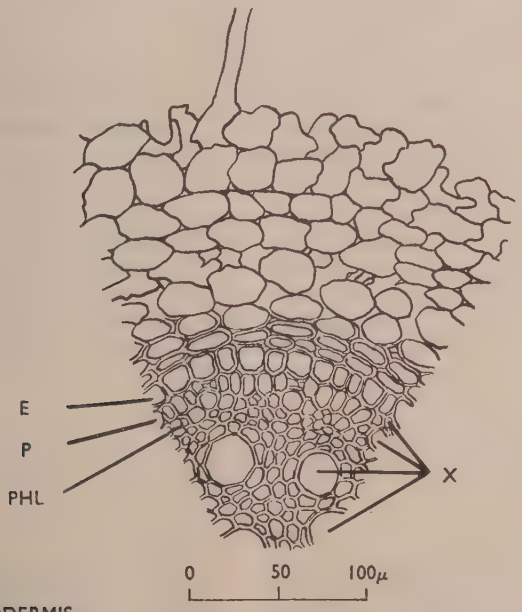


Fig. 3. Transverse section of a nodal root of *Poa pratensis* showing details of the stele. (*Diagram provided by the Landbouwproefstation en Bodemkundig Instituut T.N.O., Groningen, Netherlands*)

TABLE 4

Effect of herbage removal on character of roots

(*Biswell and Weaver*, 1933)

	Panicum virgatum		*Poa pratensis*	
	Control	Clipped	Control	Clipped
Diameter of roots (mm.)	1·5	0·96	0·38	0·29
,, steles (mm.)	0·52	0·36		
No. of metaxylem strands	7–11	5–8		
Diameter of metaxylem strands (mm.)	0·062	0·05	0·036	0·03
No. of protoxylem groups	48	32	8–11	4–6
Diameter of protoxylem strands (mm.)	0·021	0·015	0·012	0·011

in *Stipa pulchra* and *Bromus hordeaceus* by Parker and Sampson (1930) and in *Panicum virgatum* and *Poa pratensis* by Biswell and Weaver (1933) (Table 4). In Biswell and Weaver's experiment the plants were clipped at 14-day intervals from July to October, after which they were examined. Young plants of five species (*Bouteloua gracilis*, *Bromus inermis*, *Holcus sorghum*, *Poa pratensis*, and *Stipa spartea*) were found by Robertson (1933) to have reduced diameters of both root and stele as a result of clipping; these diameters in *Koeleria cristata* were however increased as a result of clipping. The reason for this discrepancy was not obvious. In four of the species adversely affected by clipping, the cortex was reduced to a greater extent than the stele, but in *Holcus sorghum* the opposite occurred. The effect of competition for their numbers. The area of the cortex decreased more rapidly with increased competition than did that of the stele (cf. Robertson's results).

The Root Cap

The root caps of South African grasses were described by Goossens (1936) as being conspicuous apical structures which when young were pale yellow in colour; as they advanced in age they became darker in colour until ultimately they could be seen as a dark speck at the root tip. In the young stage the cells were more or less rectangular, except towards the outside where they were roughly spherical with walls very much thickened. This thickening was considered by Goossens to consist of a mucilaginous substance

TABLE 5

Effect of competition on the roots of *Holcus sorghum sudanensis*

(*De Peralta*, 1935)

Criteria	Rate of seeding		
	× 3 Normal	Normal	× ¼ Normal
Diameter of root (microns)	844	1242	1772
Width of one side of cortex (microns)	190	290	426
Diameter of stele (microns)	464	662	920
Cross-sectional area of root (sq. mm.)	0·550	1·211	2·465
Area of cortex (sq. mm.)	0·390	0·867	1·801
Area of stele (sq. mm.)	0·160	0·344	0·664
Ratio of area of stele to area of cortex	1:2·4	1:2·5	1:2·7

light and water between plants of *Holcus sorghum sudanensis* was studied by De Peralta (1935) who sowed seed at the normal rate, and also at a quarter and three times this rate. The effect of the density of plant population (i.e. competition) after 7-weeks' growth is presented in Table 5. Competition had an effect similar to defoliation. The plants growing with least competition had the largest roots, due to the size of the individual cells rather than to closely related to cellulose. For the most part the root cap was separated from the root apex by a layer of mucilage of the same consistency as the cell walls.

Mucilage Secretion and the Soil Sheath.

The secretion of a mucilaginous substance by the younger portions of a root (i.e. by that portion

near the apex) has been noted to occur in grasses growing in sandy and desert environments by several workers (Warming, 1909; Price, 1911; Arber, 1934; Goossens and Stapleberg, 1933.). Price suggested that the mucilage was formed by the modification and swelling of the outer cell-walls which were being constantly renewed by the protoplasm within the cell, while Goossens and Stapleberg concluded that the formation of mucilage in the epiblem was similar to that in the root cap, where they considered that the mucilage was formed by the protoplasm in the cells. Warming, however, was of the opinion that the mucilage was secreted by the root hairs.

Goossens and Stapleberg further stated that in some species, e.g. *Sporobolus fimbriatus*, *Triraphis andropogonoides*, the mucilage became a hard, insoluble corky layer causing the roots to turn a reddish-brown colour. In the annuals which they studied (*Tragus racemosus*, *Aristida adscensionis*, *Digitaria* spp.) and the perennials of moist habitats (*Eragrostis plana*, *Cynodon dactylon*, *Paspalum dilatatum*) the mucilage occurred up to 2 cm. from the root tip, while in the more xerophytic grasses (*Themeda triandra*, *Sporobolus fimbriatus*, *Panicum coloratum*) it was found up to 10 cm. from the apex. This mucilage was thought to prevent the loss of water from the root and possibly to help in the absorption of water by the young root.

A sheath of soil particles attached to the roots of grass plants growing in dry and sandy places has been noted by several workers (Weaver, 1919; Henrici, 1929; Goossens and Stapleberg, 1933; Arber, 1934). This sheath has been attributed (a) to soil particles becoming embedded in the mucilage (Warming, 1909; Arber, 1934), (b) to soil particles adhering to root hairs (Weaver, 1919; Henrici, 1929; Goossens and Stapleberg, 1933), and to a combination of (a) and (b) (Goossens, 1936). The sheath remains on the root only as long as the cortex and so was found by Goossens and Stapleberg only on young roots and on older ones with a persistent cortex.

CHAPTER 4

ROOT HAIRS

The root hairs of grasses are particularly well developed (Arber, 1934). Dittmer (1949) in a comparison of mature plants of 37 species from 20 genera found, with few exceptions, that the Gramineae produced longer root hairs than the other species. Table 6 reproduces his results for the Gramineae together with those for a few other plant species for comparison. In earlier work, Dittmer (1938) made an intensive study of the root hairs of *Poa pratensis* (Table 7), a species which was found to produce a far greater total length of root hairs than either *Avena sativa* or *Secale cereale.*

Comparable measurements made on plants of *Lolium perenne* growing in sand culture by Richardson, S. D. (1953) showed that these plants produced shorter and fewer root hairs per unit length of root than did Dittmer's plants of *Poa pratensis*. Richardson's results indicated that root hairs on the lateral roots were longer and more frequent than on the main roots (cf. Table 7).

TABLE 6

Lengths and diameters of root hairs

(*Dittmer*, 1949)

Species	Average diameter (microns) of root hairs on roots of			Average length (microns) of root hairs on roots of		
	Main	Secondary	Tertiary	Main	Secondary	Tertiary
Agropyron elongatum (Host) Beauv.	12	12	12	800	750	750
,, *palustris* Huds.	11	11	10	900	800	800
Agrostis astoriana Auth.	13	12	12	600	600	500
,, *tenuis* Sibth.	10	10	10	400	400	300
Avena sativa L.	14	13	13	1400	1100	860
Cynodon dactylon (L.) Pers.	12	8	8	770	270	260
Eragrostis curvula (Schrad) Nees.	8	8	8	270	240	200
Festuca commutata Gaud.	13	13	12	400	400	350
Poa pratensis L.	11	9	7	1110	930	510
Secale cereale L.	15	12	12	1500	920	640
Setaria viridis (L.) Beauv.	8	8		100	100	
Equisetum arvense L.	15	15		1200	1200	
Cerastium arvense L.	12	12	10	750	600	600
Trifolium repens L.	8	8	7	250	250	200
Convolvulus arvensis L.		14	14		80	80
Plantago major L.	12	10	10	220	210	200
Taraxacum officinale Weyer		7	7		130	130

Sinnott and Bloch (1939a) and Sinnott (1939) divided the genera of the Gramineae into two main classes on the basis of the formation of root hairs on their seminal roots. In certain genera, the cells which were to form the root hairs (the

TABLE 7

Quantitative analysis of the root hairs of *Poa pratensis*; values given are the average for three soil samples each 3″ in diameter × 6″ deep (42 cubic inches)

(*Dittmer*, 1938)

Root categories	No. of hairs per mm. of root length	Total no. of root hairs (millions)	Average length of root hairs (microns)	Total length of root hairs (feet)	Av. diam. of root hairs (microns)	Total root-hair surface (sq. inches)	Volume (cubic mm.)
Main	480	25·9	1115	97,000	11	1528	2700
Secondary	88	22·8	935	67,400	9	870	1350
Tertiary	47	2·8	510	4,600	7	49	50
Totals		51·5		169,000 (32 miles)		2447 (16·9 sq. ft.)	4100

trichoblasts) were sharply differentiated at the last cell division from the 'normal' cells, and these two cell types developed very differently. In other genera, differentiation of the root-hair cells was delayed for some time and any cell, until late in its development, seemed to have the capacity to form a root hair. The trichoblasts produced root hairs at some distance back from the root tip after elongation of the cells had ceased. Early cell-differentiation was associated with:

1. Denser cell contents at the apical end of the mother cell before its division into root hair and hairless cells;
2. Unequal division of this mother cell, the smaller daughter cell (the one that produces the root hair) lying toward the apex and retaining denser cytoplasmic contents for a considerable time during subsequent extension;
3. The origin of the root hair near the apical end of the cell in a relatively constant position;
4. A forward growth of the root hair at an acute angle with the root axis.

Conversely, where differentiation was late, the cell contents of the mother cell were of equal density throughout; the division of this mother cell was essentially equal so that there was less regular alternation of root hair and hairless cells; the hair originated from near the middle of the cell at right angles to the root axis. Early cell differentiation occurred in *Phleum pratense*, *Poa pratensis* and *Agrostis* spp. and late differentiation in *Sporobolus cryptandrus*, while *Chloris gayana* was intermediate in this respect. More recently Reeder and von Maltzahn (1953) have suggested that early differentiation is characteristic of the Festucoideae and late differentiation of the Panicoideae. For this to be the case certain changes from the traditional classification would have to be made, changes which Reeder and von Maltzahn stated are supported by embryological, anatomical and cytological evidence.

Both Sinnott (1939) and Brumfield (1942) noted that trichoblasts grew at a slower rate than other cells. Brumfield stated that in *Phleum pratense* the growth rate of the trichoblasts increased more gradually than that of the hairless cells during the transition from protoplastic synthesis to vacuolation.

Cormack (1944) confirmed the findings of Sinnott and Bloch (1939a) regarding the position of origin of the root hair in cells of *Phleum pratense* and *Sporobolus cryptandrus*, namely, that in *Phleum pratense* the mature hair occupied a constant position at the apical end of the cell, while in *Sporobolus cryptandrus* it may be found near the middle of the cell or at the apical end. Sinnott and Bloch explained this difference on the basis of cell polarity, assuming a strong apical tendency in the formation of root hairs in the epidermal cells of *Phleum pratense* and a very much weaker one in *Sporobolus cryptandrus*. Cormack put forward the explanation that in *Sporobolus cryptandrus* longitudinal elongation of the hair-forming cell continued to occur after the papilla had started to push out, resulting in the papilla occupying a more central position.

The formation of root hairs in *Phleum pratense* was described by Cormack as being a continuation of cell elongation. Through the gradual hardening of the cell wall longitudinal elongation was arrested, and, due to increasing pressure from within, the wall was pushed out at its softest point, invariably at, or near, the apical end of the cell. At this point elongation continued, but in a new direction, and a long narrow hair resulted. The formation of root hairs was, in Cormack's opinion, controlled by the changes in the cell which produced a progressive hardening of the epidermal walls, the hardening process involving a change from pectic acid to calcium pectate in the middle lamella. This change was influenced by the pH of the culture solution and the status of the calcium nutrition. In culture solutions under most conditions short cells were able to effect the calcification of their cell walls at an early stage and thus form root hairs. The long cells were unable to do this and remained hairless. Under conditions which facilitated more rapid calcification (plenty of calcium and a slightly alkaline medium), all cells formed root hairs. Under conditions that brought about too rapid calcification (plenty of calcium and a strongly alkaline medium), root hairs were not produced, while, due to the interaction of neighbouring cells, the epidermal cells became separated and their walls broken. Under conditions that retarded calcification, (insufficiency of calcium and a slightly acid medium) longitudinal elongation was promoted, while root hair production was decreased. *Sporobolus cryptandrus* roots responded to the various culture solutions in a similar manner to *Phleum pratense*. It is of interest that Goossens and Stapleberg (1933) stated that, of the essential elements, calcium seemed to have the greatest influence on the development of root hairs.

The growth of the root hair itself was studied in *Phleum* sp. by Jensen (1954). He stated that the cytoplasm in the root hairs consisted of streaming granulated plasma which was surrounded by a thin, clear layer of plasma, the hyaloplasm. From this, papillae or crests of plasma protruded into the cell wall in the tip of the root hair. Elongation arose through the co-operation of two factors, viz. turgor pressure and intersusception, i.e. production of new cellulose fibrils by cellulose-building enzymes on the surface of the papillae. As these were localised in definite places in the cell wall of the tip, growth took place at a certain moment at many sharply defined spots. Through the activity of the cellulose-building enzymes the hollows in which the papillae were situated were filled out by cellulose fibrils and enlarged. In consequence of turgor pressure and growth, new channels and hollows arose, especially in the extreme tip of the cell wall. In these hollows new papillae protruded, and thus the growth places were shifting incessantly. There was a strong adhesion between the plasma in the cell wall and the substances of the cell wall. By different means, Congo red, weak plasmolysis, and so on, this adhesion could be broken down and the plasma with the cellulose-building enzymes withdrawn from the cell wall. The enzymes continued to build cellulose, the cellulose fibrils being deposited on the inner side of the cell wall, and so thickening took place, i.e. the elongation was changed to a thickening growth.

Environmental factors other than those mentioned previously, pH and calcium nutrition, have been found to influence the development of root hairs. Devaux (cited by Farr, 1928) found that, in the presence of light, the root hairs of *Lolium* spp. and other grasses showed a daily periodicity of growth. He thought that more and longer hairs were formed in the light than in the dark, with the result that a cone-shaped mass of root hairs was formed daily. Goossens and Stapleberg (1933) observed similar cones on roots of *Eragrostis plana* but were of the opinion that these were the result of daily fluctuations in temperature. The daily changes in growth could be correlated with the daily changes in temperature, and likewise the root hairs formed during winter were shorter than the corresponding ones formed during summer. Plants grown in the dark showed this cone-shaped development, which rather discounts Devaux's theory. At low temperatures, and also when phosphorus was absent from the culture solution, the root hairs attained various shapes instead of being long and cylindrical.

The root hairs of South African grasses grown in a fairly dry soil or in an atmosphere of high humidity were stated by Goossens (1936) to be longer than those grown in watery solutions and wet soils. This is in agreement with the statement of Cormack (1944) that the root hairs of *Sporobolus cryptandrus* were sparsely developed in aqueous solution as compared with those formed in moist air. The results of Nishimura (1922) showed that the root hairs of *Phleum pratense* and *Poa pratensis* were shorter when grown in water than when grown in moisture-saturated air.

Parker and Sampson (1930) observed that root hairs were not produced after the first month of growth by plants of *Stipa pulchra* and *Bromus hordeaceus* growing in water culture when the plants had their shoot growth removed by clipping. Root hairs were produced by non-defoliated plants of *Stipa pulchra*, and appeared a short distance behind the meristematic region of the root tip; they died as newer root hairs were formed. The roots of non-defoliated plants of *Bromus hordeaceus* produced root hairs when they were very young but were later devoid of them. Parker and Sampson considered that this disappearance of root hairs might have been due to the accommodation of the species to the oxygen supply. Bittera and Grúber (1938) found that root hairs were formed during the first period of development only, and then only to a small extent, by plants of *Agropyron cristatum* growing in culture solutions lacking phosphorus and nitrogen.

The root hairs of grasses tend to be persistent (Arber, 1934; Eames and MacDaniels, 1925). Goossens (1936) reported that in some South African grasses the root hairs persisted for many years and were found over the whole length of the root. Persistent root hairs have been reported in some members of the Leguminosae by McDougall (1921) and in several members of the Compositae by Whitaker (1923). Both these workers stated that the persistent root hairs were brown in colour and possessed a thick wall. Henrici (1929) thought the persistent root hairs of South African grasses resembled those described by McDougal, but Goossens and Stapleberg did not find any evidence of thick walls or brown

coloration. They stated that even the root hairs of *Sporobolus fimbriatus*, which has a suberised epiblem, had thin cellulose walls. Weaver (1919) pointed out that root hairs may persist over the whole length of a grass root but did not mention a brown colour or thick walls. The persistency of root hairs may contribute greatly to a root's ability to absorb water and nutrients.

Jacques (1937a) described the distribution of root hairs on the three types of nodal roots which he distinguished in *Lolium perenne* and *Cynosurus cristatus* (p. 9). None had truly persistent hairs but young 'white' roots retained hairs over the whole of their length until they started branching. Root hairs were apparent on the 'fibrous' and 'intermediate' roots only immediately behind the points of elongation. In a later paper, Jacques (1939) described the formation of secondary root hairs on the 'white' roots of *Lolium perenne*, *Festuca rubra* var. *fallax*, *Bromus unioloides*, and *Agrostis tenuis*. These hairs were formed on the part of the root near to the crown of the plant and did not necessarily arise acropetally, as did the primary root hairs. No particular stimulus could be found to explain their development. That these root hairs were secondary, and not persistent primary ones, was demonstrated by the observation that the region behind the active primary hairs was devoid of root hairs and that they subsequently reappeared on the older portion of the root.

CHAPTER 5

UNDERGROUND ORGANS OTHER THAN ROOTS

Rhizomes and Stolons

There is considerable confusion in the nomenclature of these organs. Oakley and Evans (1921) have suggested a fourfold classification as follows:

1. Determinate rhizome. An underground stem which is disposed to root at the nodes and from which a single aerial shoot or tuft of shoots is produced, e.g. *Poa pratensis*.
2. Indeterminate rhizome. An underground stem, thickened or unthickened, which roots at the nodes and produces aerial shoots progressively, e.g. *Agropyron repens*.
3. Determinate stolon. An above-ground stem which roots at the nodes but which does not produce aerial shoots progressively. Under this heading is included lax culms that have come into contact with the soil and rooted at the nodes, e.g. *Paspalum dilatatum*, *Syntherisma sanguinale*. This type of rooting stem is common in some species of *Agrostis*, e.g. *A. alba*; such grasses, however, also have indeterminate stolons.
4. Indeterminate stolons. An above-ground stem which roots at the nodes and from which shoots are produced progressively, e.g. *Cynodon dactylon*, *Chloris gayana*.

This publication is theoretically concerned with the first two types, but as considerable practical difficulty is experienced in distinguishing between rhizomes and stolons, and their functions are roughly the same, the information available regarding both types of rooting stem has been considered.

The functions of rhizomes and stolons are vegetative reproduction and the storage of food reserves. Species vary greatly in their ability to produce these organs (Kannenberg, 1931). Species which do not normally produce rooting stems may do so when growing in unusual conditions, e.g. *Phleum pratense* will do so when its young growing culms are covered with soil (Oakley and Evans, 1921).

A great deal of variation was found by Evans and Ely (1935) in the way rhizomes were developed by different species. In some, e.g. *Poa compressa*, secondary and later rhizomes originated from buds at nodes on older rhizomes at more or less regular intervals. In other species, e.g. *Poa pratensis*, a very large proportion of the rhizomes arose from buds in the bases of above-ground shoots. This latter observation agrees with that of Etter (1951) who described the rhizome of *Poa pratensis* as originating from the axils of dead or dying leaves and protruding through the base of the sheathing leaf if it was still attached to the plant.

The tip of the rhizome of *Poa pratensis* was described by Etter (1951) as resembling a sharp white awl with a minute pore at the tip. The cataphyll, i.e. a leaf without a blade or a scale leaf, which formed the tip of the rhizome, served as a caisson in which new cataphylls were formed. A new cataphyll emerged from the surrounding sheath of the older one by penetrating it; the older cataphyll then split and dried up. An axillary bud was found in the axils of most cataphylls. A pair of roots was usually produced at each node. Growth took place through the elongation of both the cataphylls and the stem separating them. The first two or three internodes nearest to the parent plant were quite short, the next few intermediate in length and the rest of any length within a wide range, apparently depending largely upon the amount of water available to the plant (Etter was working in Missouri). The sequence of cataphyll lengths was essentially similar to that of the internodes. The formation of aerial shoots was preceded by the modification of cataphylls to the normal long-bladed leaf. Etter was of the opinion that the change in direction of the rhizome from horizontal to vertical was due to the action of these leaf blades growing in the opposite direction to gravity.

In *Agropyron repens* and *Sporobolus virginicus* it was observed by Palmer (1954) that aerial-shoot formation was preceded by a change in the response of the rhizome to gravity, the tip becoming negatively geotropic and curving into a vertical position. A rhizome could be induced to change prematurely into an aerial shoot by placing the rhizome so that it pointed vertically upwards.

In *Poa pratensis*, Etter (1951) noted that the rhizomes produced during the summer extended some distance away from the plant before they produced aerial shoots but those produced at other times of the year, especially if produced

as a result of injury to the plant, were much shorter.

Rapp (1947) stated that small pieces of *Sorghum halepense* rhizome lost weight for the first thirty days after detachment and placing in soil. Thereafter they gained weight, except during periods of rapid shoot-growth. The weight of roots increased at first, as they were being formed, but then became constant, possibly due to the plants being grown in pots.

Corms and Bulbs

The formation of bulbs and corms by grasses was studied by Häckel (1890) and more recently by Burns (1946). The latter stated that bulbs and corms were formed in the following genera:—

Poa, *Melica*, *Molinia*, *Festuca* (?), *Holcus*, *Arrhenatherum*, *Beckmannia*, *Hordeum*, *Alopecurus*, *Phleum*, *Ehrharta*, *Phalaris*, and *Panicum*.

All the corms examined by Burns were swollen internodes on the the lower part of the culm, sometimes one only being swollen and sometimes a chain of them. Various shapes of corms occurred, and they were often protected by the dead sheaths of old leaves—'tunics'. The cross-sections examined showed the following common characteristics:

1. A small-celled epidermis with a marked cuticle.
2. A cortex of two or three layers of cells.
3. A band of sclerenchyma with vascular bundles in it.
4. A central cylinder of fundamental tissue with larger vascular bundles, mainly towards the periphery and sometimes in two irregular rings (Fig. 4).

Häckel (1890) was of the opinion that the main function of these organs was the storage of water, but modern opinion supports the view that their main function is food storage. Evans, M. W. (1927) suggested that the haplocorm of *Phleum pratense* contained a store of nutrients for use during growth in the summer, while Waters (1915) was of the opinion that their function was to store food which would give an early and vigorous start to spring growth in the next year. A

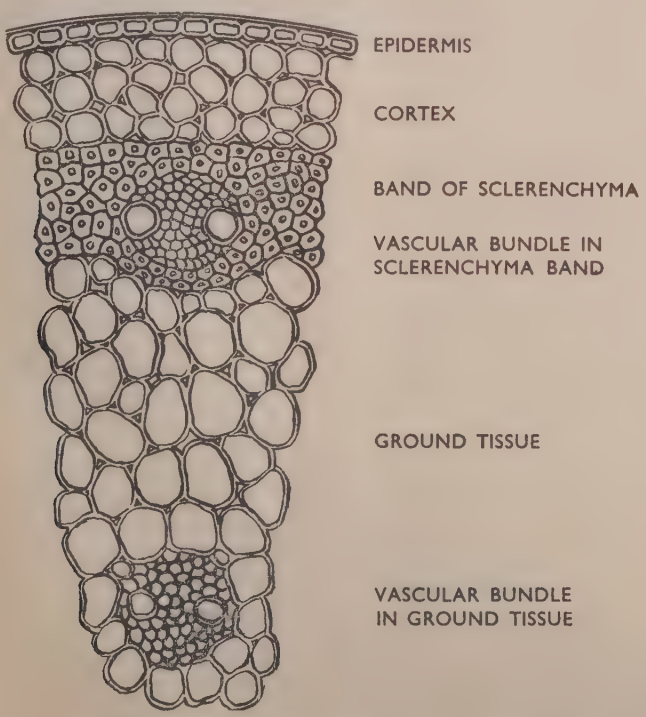


Fig. 4. Transverse section of a haplocorm of *Phleum pratense*. (*Burns*, 1946)

similar opinion, namely that the haplocorm is especially concerned with the development of shoots in the following year, was expressed by Nishimura (1922). Jefferies (1916) stated that the club-shaped basal internodes of *Molinia caerulea* contained a store of food which was utilised for early spring growth and the corms of *Arrhenatherum avenaceum* were considered by Jenkin (1931) to be a means by which the plants overwintered. The idea that corms and bulbs act as food stores is supported by the data on chemical composition (pp. 53–4). Corms and bulbs may also act as organs of propagation (Weaver and Clements, 1938; Waters, 1915; Evans, M. W., 1927). The roots of *Poa bulbosa* were reported by Plummer (1943) to dry up in the summer under the hot, dry conditions of Utah, subsequent growth depending upon the new roots produced by the plants' 'bulblets'.

Burns (1946) stated that most of the corm-forming species of grasses are found where a Mediterranean climate exists. Some occur in steppe or semi-desert while a few are swamp plants. He concluded that corms and bulbs in the Gramineae are devices for tiding over the hot, dry season of the Mediterranean climate and for giving plants a flying start when the growing season recommences. In a few cases the cold season is overcome by the same means.

Leaf Bases

Some species of grasses have enlarged leaf-bases which function as storage organs of food materials. Jones (1933a) noticed that leniently grazed plants of *Dactylis glomerata* exhibited characteristic succulent white leaf-bases weighing 19,870 lb. per acre, whereas in closely-cut plants they weighed only 2,978 lb. per acre. That these white leaf-bases from the leniently grazed plants contained reserve substances was shown by placing a portion of them (detached from both leaf and root) in a glass jar at room temperature; there was immediate production of young leaves which turned green within two days and continued growing for at least a fortnight, producing 4 in. of leaf. These new leaves resembled those produced after severe defoliation. Häckel (1890) observed that grasses growing in dry climates often had their lower internodes protected by leaf sheaths, and gave the name 'tunika' (tunic) to this type of covering.

CHAPTER 6

GROWTH OF THE YOUNG PLANT

During the first few months of a plant's life, if it is in a suitable environment, the root system grows very rapidly, the growth rate increasing from zero just before germination to a maximum some weeks later, after which it decreases. The growth of the roots consists of an increase in their numbers, weight and length, and varies considerably between species.

TABLE 8

Daily increase in length (cm.) per plant of the root systems of plants of three species

(*Pavlychenko*, 1942)

Interval (in days)	0–5	5–15	15–30	30–60	60–90
Length of interval (in days)	5	10	15	30	30
Agropyron cristatum	7	7	169	4476	6840
Agropyron pauciflorum	8	24	263	4797	7980
Bromus inermis	6	7	175	4051	6485

The rate of increase in root length of plants of three species was measured by Pavlychenko (1942) (Table 8). Kauter (1933) in Zurich found that the number, length and weight of roots all increased during the growth of the young plant. The 'early' species in his investigation (*Lolium italicum* and *Arrhenatherum elatius*) were deeper rooting and produced a greater weight of roots than the 'late' species (*Phleum pratense* and *Festuca pratensis*) during the first few months of growth (Tables 9 and 10). Troughton (1954) working in Wales with plants from five to fifteen weeks after sowing and Sprague, V. G. (1943) working with plants grown in artificial 'constant' environments from two to seven weeks old have also noted an increase in weight of roots during the growth of the young plant. In Kauter's experiment the distribution of the weight of the plants between root and shoot showed no consistent trend between the third and fifth month; nor did the weight of root per tiller and the number of roots per tiller. The percentage of the plant's weight in the roots decreased in Troughton's experiment. In Sprague's experiment the results were very variable, but there was a tendency for a slight increase in the percentage of the plant's weight in the roots.

From a study of range grasses, Plummer (1943) concluded that the root development during the first three months was directly associated with the seedlings' initial success or failure. Those species that he studied which had slow root development (*Agropyron smithii*, *Elymus triticoides simplex*, *Festuca ovina* and *Stipa arida*) were the species which were extremely difficult to establish, while species like *Arrhenatherum elatius* and *Bromus inermis*, which developed roots much more rapidly, established early stands much more successfully, although they may later have succumbed to the rigours of a drier site where such

TABLE 9

Dry weight of roots per plant in grams and percentage of the weight of the plant in the roots when 3, 5 and 12 months old

(*Kauter*, 1933)

	3 months		5 months		12 months	
Species	Root wt.	Percentage of weight in roots	Root wt.	Percentage of weight in roots	Root wt.	Percentage of weight in roots
Lolium italicum	1·30	31	2·21	30	4·57	23
Arrhenatherum elatius	1·49	30	2·73	30	5·23	29
Festuca pratensis	0·49	38	1·26	38	5·36	24
Phleum pratense	0·29	37	0·79	32	2·40	16

TABLE 10

Number of tillers and roots, and total length of roots per plant of four species when 3, 5 and 12 months old

(*Kauter*, 1933)

	Lolium italicum	*Arrhenatherum elatius*	*Festuca pratensis*	*Phleum pratense*
3 months				
Tillers	14	18	8·5	6
Roots	84	110	67	42
Length (in m.)	14·8	18·6	9·1	5·3
5 months				
Tillers	19	27	16	11
Roots	182	128	102	66
Length (in m.)	30·4	33·5	22·2	11·5
12 months				
Tillers	33·5	22	39	13
Roots	356	180	292	170
Length (in m.)	79·7	52·0	60·0	31·6

species as *Agropyron smithii* and *Stipa arida* would have continued to grow and propagate had they been able to gain a foothold. The more universal success of *Agropyron cristatum* Plummer attributed, in a large part, to its ability to produce a greater total root-length in the seedling stage than any of the other species. Simpson and Moore (1955) in New Zealand noted that while young seedlings of *Agropyron* and *Bromus* spp. were killed during the winter by ice lifting them out of the ground and severing the roots, the seedlings of *Poa lindsayi*, a species which produced a great number of slender roots, survived.

Differences between strains of *Bromus inermis* during the first season's growth were investigated by Cook (1943) who found that some strains produced a relatively large number of roots early in the season while others did not do so until the middle or the end.

TABLE 11

The average measurements of ten typical plants of *Phleum pratense* sown each month and measured November 26th

(*Nishimura*, 1922)

Date sown	Number of shoots	Length of crown roots		Number of crown roots
		Longest (cm.)	Average (cm.)	
April 26th	5	12·8	7·7	32
May 26th	6	12·8	9·0	42
June 26th	5	13·0	8·0	40
July 26th	4	11·5	6·4	22
Aug. 26th	3	7·7	3·9	12
Sept. 26th	1	3·9	2·6	6
Oct. 26th	1	1·6	7·0	4

The effect on the plant of variation in the time of sowing in the spring was studied by Nishimura (1922) (Table 11). By the autumn of the year of sowing those plants developed from seed sown in April, May and June showed the same degree of development while plants developed from July to October sowings showed progressively decreasing growth. The plants from the September and October sowings were killed by frost during the following winter (the work was carried out in Columbia, USA) and the August-sown plants were so retarded that they did not flower in the following summer. Similar results were obtained with both *Poa pratensis* and *Phleum pratense*.

The effect of time of sowing upon root development was also studied by Jacques (1941). Seeds of *Lolium perenne* and *Trifolium repens* were sown in the autumn and the spring, the resulting swards being either grazed or mown for hay in the following growing season and the root systems examined in the autumn. The autumn-sown grazed plots yielded a greater root weight in the deeper (36–72 in.) soil layers than the spring-sown grazed plots, while the spring-sown hayed plots yielded a greater total root weight, with better root penetration, than the autumn-sown hayed plots. This, Jacques suggested, was due to the failure of the spring-sown plants to develop seed heads. In Germany, Könekamp and Zimmer (1955) found that the mean weight of the roots of *Lolium perenne* was higher in the year after sowing when the sowing was carried out in May than in July. With *Lolium italicum* no difference was apparent in the root weights.

A young plant needs to have a well-developed root system before it is subjected to adverse environmental conditions if it is to survive. Keim and Beadle (1927) found that with autumn sowing in Nebraska it was the plants with vigorous, well developed root systems which survived the winter. The root system of the plants they studied varied with the species and the time of sowing. Robocker, Curtis and Ahlgren (1953) suggested that the drought resistance of *Bouteloua gracilis* compared with other native grasses was possibly due, in part, to its rapid development of seminal roots and the more extensive growth of its roots, rather than its shoots, when young.

The first few months of growth provides a very suitable opportunity for the study of the relative growth of the roots and shoots in grass plants, as the measurement of root growth is not hampered by the presence of old decaying roots.

Troughton (1955b and 1956) stated that the relationship between the root- and shoot-weight of young grass plants in several experiments carried out by him could be expressed by the allometric formula. This formula could be written $y=bx^k$ when y represents the weight of the roots, x the weight of the shoots, b a constant equal to the value of y when the value of x was unity and k a constant equal to the ratio

$$\frac{\text{logarithmic growth rate of } y \text{ (roots)}}{\text{logarithmic growth rate of } x \text{ (shoots)}}.$$

The values of x and y were obtained by weighing plants at intervals over a period of time. The values of b and k were then obtained by calculation or by graphical means. When the relationship between two series of values can be expressed by this formula, then the points produced on a graph by plotting their logarithmic values against each other will lie along a straight line.

A comparison of the values of k calculated for different series of plants enabled the effect of environmental and genetic factors upon the relative growth rates of the roots and shoots to be assessed. Troughton (1955b) has pointed out the advantages of this mode of comparison of root and shoot growth as against the more usual method of comparing proportions of plants, e.g., root : shoot ratio, percentage of the plant's weight in the root. When using the latter method differences may be due to variations in the size of the plants, as well as to the experimental treatments. Troughton (1954) had previously pointed out that in one experiment, the proportions of root and shoot in young plants changed as the plants increased in size.

Differences in the value of b between experimental treatments indicated either variations in the value of k between the treatments prior to the first measurement, i.e. prior to the period of measurement, or to variations in the size of the plant at which the factors influencing the value of k during the period of measurement became operative.

The use of the allometric formula has the disadvantage that plants must be measured on at least three occasions; on this account it cannot be applied to most of the results reported in the literature, as in these experiments the plants were measured on one occasion only.

The relationship between root and shoot growth, as measured by increase in weight and the number of tillers in young grass plants, was studied by Troughton (1955a). Young plants growing both in pots and in the field were noted suddenly to cease production of new tillers, while the increase in weight of root and shoot was almost unaffected. Thus the relationship between root weight and number of tillers is apt to be variable.

CHAPTER 7

THE SEASONAL GROWTH CYCLE

Once a plant has become established, then, under natural conditions, its growth becomes controlled by the seasonal cycle of environmental growth factors, both shoot- and root-growth being affected by these changes.

The components of the seasonal growth-cycle of the root system are the initiation and growth of roots, the decay of old roots and the use the plant makes of the root as a storage organ for food reserves.

Initiation and growth have been most frequently observed during autumn and spring: in relatively mild climates it has also been observed during the summer and winter. Most root growth apparently takes place during the spring, the maximum growth being reached before that of the herbage and ceasing altogether before the time of flowering. Usually little further growth then seems to take place until the autumn. Old roots start to decay about the time the plants flower. The seasonal cycle may be altered by severe defoliation (p. 94 *et seq.*).

Initiation

While studying the effects of root pruning upon plants of *Lolium perenne* and *Dactylis glomerata* in New Zealand, Jacques and Edmond (1952) found that the initiation of new roots proceeded slowly from the time the plants were transplanted into the field in autumn (March) until mid-winter (July). Then followed a period of great activity until the late spring (September), after which there was a large decrease in the rate of initiation during the summer. There was a slight increase followed by a decrease from December to February.

Maximum root initiation occurred at a time when herbage growth was generally slow, viz., winter to early spring, while maximum herbage growth occurred at a time when the rate of root initiation was very low, viz., mid-spring to mid-summer (mid-September to mid-December).

In this experiment the new roots were cut off as they were formed so that the plants were stimulated to produce more roots than they would have done normally, but this does not necessarily detract from the value of the experiment in indicating at which time of the year the plants initiated most roots. (See also pp. 103–4).

These results are to some extent confirmed by the work of Schwass and Jacques (in press). These workers found in *Lolium perenne* and *L. italicum* plants that root initiation occurred during the winter, during which period shoot growth was slow. This however was not so with plants of *Festuca arundinacea*. The shoot growth of plants of this species was not so curtailed at either end of the winter period as it was in the plants of the *Lolium* spp. but the *Festuca arundinacea* plants still initiated roots steadily throughout the winter so that roots were initiated while shoot growth was active.

Stuckey (1941), in Rhode Island, USA, found a similar distribution in the time of root initiation in nine temperate grass species. New roots were produced during October, November and December; during January and February the soil was frozen and no plants were examined during January, but, in February, six species produced new roots. The soil thawed by 1st March, and, during this month and the next, the development of new roots was very conspicuous, reaching a maximum during the first two weeks of April and ceasing about the time the flower primordia became visible in May. Stuckey suggested that this cessation may have been due to the developing flower primordia inhibiting the production of new roots (Fig. 5).

In New Jersey, Sprague, H. B. (1933) noted the production of new roots by *Poa pratensis* and *Agrostis tenuis* during the spring and thought it was closely related to temperature. Etter (1953) working in Missouri noted that a slight rise in soil temperature in February resulted in the production of new roots by a *Poa pratensis* sward. Production of new roots apparently continued until April. They were also produced in autumn. These new roots Etter described as being fat and white in comparison with the slender, wiry roots he observed in the summer.

Growth

In Rhode Island, Stuckey (1941) used the presence of dividing cells in the root tip, together

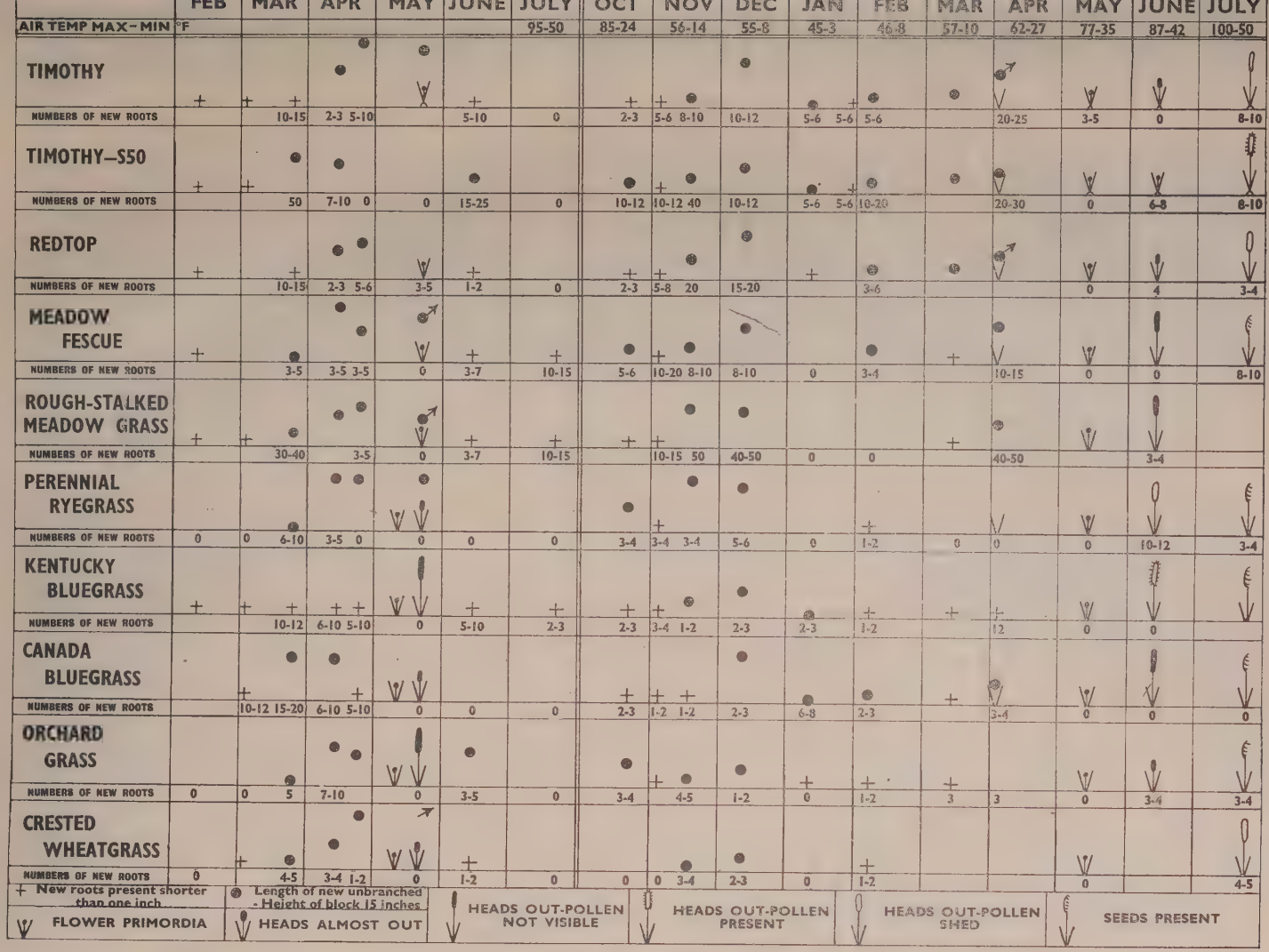


Fig. 5. The seasonal growth cycle. (*Stuckey*, 1941)

Timothy = *Phleum pratense*
Red Top = *Agrostis stolonifera*
Meadow Fescue = *Festuca pratensis*
Rough-stalked Meadow Grass = *Poa trivialis*
Perennial Ryegrass = *Lolium perenne*
Kentucky Bluegrass = *Poa pratensis*
Canada Bluegrass = *Poa compressa*
Orchard Grass = *Dactylis glomerata*
Crested Wheatgrass = *Agropyron cristatum*

with visual observations, as the criteria for determining the occurrence of growth in the roots of temperate grasses. In the species with 'annual' roots (p. 36) the whole root system was regenerated each year, active production of new growth beginning in October, continuing slowly throughout the winter and increasing rapidly after the spring thaw in March to reach a maximum in April. After the middle of June, few, if any, new roots were formed and there was no appreciable growth of existing roots until October. In plants of the species with 'perennial' roots the development during the first year was essentially the same, but, after the first spring, a few new roots only were developed. Root tips were found dividing at temperatures very close to 32°F., and the cessation of growth during the summer coincided with a period of high soil-temperature.

The weight of underground organs in the soil of fields under grass was found by Troughton (1951) to increase from November until May in the mild climate of west Wales. In a climate with greater extremes, viz., Utah, McCarty (1938) and McCarty and Price (1942) noted three periods of nodal root-growth in *Bromus carinatus* and *Agropyron trachycaulum*. These were at the close of the summer period of shoot growth (August), at the end of the snow-free period in autumn (October) and immediately preceding the snow's disappearance in spring (April). Brown, E. M. (1943), in Missouri, was of the opinion that autumn and spring were the most favourable seasons for the root growth of an established sward of *Poa pratensis*, early spring with a soil temperature of 40–60°F. being the most favourable. During the summer the roots produced no growth, or actually lost weight, the soil temperature then being approximately 80°F.

Under Californian conditions, the autumn (November and December) was the only time when active development of the main nodal roots of *Stipa pulchra* was noted by Sampson and McCarty (1930), although lateral root growth may have taken place at other seasons. Könekamp and Zimmer (1955) in Germany noted increases in the weight of roots under swards of *Lolium perenne* and *L. italicum* during September and October, after which month no further measurements were made.

Growth was found, by Troughton under Welsh conditions, and to a more limited extent by Stuckey in Rhode Island, to continue during the winter. Under Swiss conditions, Kauter (1933) found that the young plants of eight species* all made considerable root growth from December to March, and this did not cease even when the surface of the ground was frozen. Stuckey also noted root growth near 32°F. Kauter was unable to correlate the amount of root growth of the different species with their winterhardiness or vigour of shooting in the spring. The species (*Lolium italicum* and *Arrhenatherum elatius*) which showed marked signs of aerial activity during the winter were also distinguished by a more vigorous root growth.

Root growth in spring, as well as being observed by Stuckey, Brown, and Troughton, was also noted by Goedewaagen and Schuurman (1950a) in the Netherlands, Könekamp and Zimmer (1955) in Germany and by Sprague, H. B. (1933) in New Jersey. Goedewaagen and Schuurman stated that the total amount of roots of leys increased from early spring until May. Increases in the root weights of swards of *Lolium italicum*, *L. perenne* and permanent grassland were found by Könekamp and Zimmer from March, when the root weights were first determined, until April or early May. Sprague was of the opinion that root growth at this time of the year was closely related to the temperature; *Poa pratensis* was apparently able to grow at lower temperatures than *Agrostis tenuis*, as the former started growth in the spring, ceased the formation of new roots and flowered earlier than did the latter. Apparently both passed through the same physiological phases, but *Poa pratensis* did so at lower temperatures than *Agrostis tenuis*. Under these conditions approximately half the root system of both species was regenerated each spring. The longest roots of plants of *Lolium perenne* were found by Roberts and Hunt (1936) to reach their maximum length a month or so before the plants attained their maximum root-weight. This indicates that an increase in root-weight during the late spring was probably due to either the growth of the branches or an increase in cell contents.

Growth has not been frequently noted during the summer, although it may occur and be masked at this time of the year by the decay of old roots. Baker, H. K. (1955) in England found that the root weight of infrequently defoliated young

* The species were *Lolium italicum*, *Arrhenatherum elatius*, *Festuca pratensis*, *Phleum pratense*, *Alopecurus pratensis*, *Trisetum flavescens*, *Dactylis glomerata* and *Agrostis alba*.

swards of *Lolium perenne* increased from early spring until autumn during the year after sowing, and in Wales the root weights of moderately defoliated spaced plants of *Dactylis glomerata* were noted by Stapledon and Milton (1930) to increase progressively from May to September. In Germany, Könekamp and Zimmer (1955) noted increases in the root weight of a sward of *Lolium perenne*, and in permanent grassland in July and August. A significant increase in the dry matter of the roots of *Chloris gayana* was found by Weinmann (1940b) to occur after the time of flowering and during the formation of the seed. Both Stuckey and Brown, E.M. (1943) commented upon the fact that cessation of root-growth in summer coincided with high temperatures (75–80°F.) in the upper few inches of the soil.

Decay

In Russia, Čepikova (1942) found that as spring advanced, the roots of *Festuca pratensis*, which had been produced the previous year, became darker and more easy to tear while the colloids of the living tissue diminished in volume and the enzyme catalase became less active. With the cessation of catalase activity the root system was considered to have died and this stage was seen to coincide with that of the most active herbage growth of the plants, i.e. when the inflorescences were emerging and photosynthesis was at its maximum (Table 12). The disintegration of roots produced the previous season was stated by Stuckey (1941) to take place during June, when the growth of new roots had almost ceased and the plants were flowering. This is in agreement with the observations of Čepikova.

Both Goedewaagen and Schuurman (1950b) and Troughton (1951) considered that under European conditions the decay of roots under swards took place from May until sometime in the winter, resulting in a loss of weight by the root system as a whole. Troughton (1951) working with mixed swards composed chiefly of *Lolium perenne*, *Poa trivialis* and *Agrostis* spp. found that the weight of underground organs decreased from July until November. The results of Könekamp and Zimmer (1955) in Germany indicated that the root weight under a sward of *Lolium italicum* decreased from April or May until August, while the weight under a sward of *Lolium perenne* decreased from April until July and again in August. Kübler (1954) who was also working in Germany noted a decline in root weight from the beginning of herbage growth until sometime after July. Baker, H. K. (1955) working with *Lolium perenne* in England noted a decrease in root weight from August to January, after being sown in the previous February, but in the next year no decline was evident by November when the observations ceased. In Missouri, the roots of *Poa pratensis* were noted by Brown, E. M. (1943) to decay during the summer (July to September), the decay apparently being intensified by irrigation during times of drought.

Premature decay of roots may follow an attack by fungi of the *Pythium* spp. These fungal species, which cause browning root rot of cereals, have been found to cause a similar disease in herbage grasses. Young roots whether belonging to a seedling or to an older plant were reported to be particularly susceptible to attack (Vanterpool, 1942).

TABLE 12

Changes in the roots of *Festuca pratensis* (*Čepikova*, 1942)

Date	Growth stage	Colour	Durability	Imbibing capacity of colloids	Activity of catalase (in ml. $KMnO_4$)
April 20–23	Beginning of vegetation	grey/tawny	great	19·9	11·5
May 2–5	Tillering phase	grey/tawny	great	15·1	9·3
May 10–14	Tillering phase	tawny	small	12·5	9·1
May 20–25	Beginning of stooling	tawny	weak	10·6	4·2
June 2–5	Stooling to beginning of earing	dark tawny	—	—	0·5

Root- and Shoot-Growth

No worker has reported that the maximum growth of both roots and shoots coincide in an experiment in which these were measured at frequent intervals. McCarty (1935, 1938) and McCarty and Price (1942) observed root growth to take place during the closing stages of herbage growth and before the herbage started growth in the spring. Stuckey (1941) noted root growth to take place in the autumn, winter and spring, the peak of root growth in the spring occurring before that of shoot growth. In Roberts and Hunt's (1936) experiment with *Lolium perenne* and *Phleum pratense* the highest weight of roots per plant was attained before the highest weight of shoot. The relationship between shoot growth and root initiation is discussed on page 30.

In some investigations a loss of root weight, which may be connected with the withdrawal of food reserves for use in herbage growth, has been noted (p. 49 *et seq.*). Troughton (1951) noted a short-lived depression in the weight of underground organs of a mixed (*Lolium perenne*/*Poa trivialis*) sward during April which he attributed to early shoot-growth. A decline in the root-weight of a *Poa pratensis* sward was noted by Sprague, H. B. (1933) during May at a time of rapid shoot-growth. This decline was followed by a gradual recovery.

Periods of emergence of flowers were found by Baker, H. K. (1955), working with *Lolium perenne*, to be associated with reductions in the rate of increase in root weight. Troughton (1955b, 1956) noted that the production of flowers resulted in a reduction of the growth rate of the roots compared with that of the shoots for some time prior to the emergence of the flowers. Growth was expressed as increase in weight, and several species were studied.

Rhizomes

There seem to be few common features between the accounts of the seasonal cycle of rhizome growth. Cates and Spillman (1907) defined the primary rhizomes of *Sorghum halepense* as those which were alive in the ground at the beginning of the growing season. During the spring and summer these rhizomes produced secondary ones which came to the surface and formed crowns, so producing new plants. Tertiary rhizomes were those produced later in the season from the base of the new plants. During the autumn, the primary rhizomes decayed, the secondary and tertiary rhizomes of one season becoming the primary ones of the next.

Working with *Poa pratensis*, *Poa compressa*, *Agropyron repens*, *Agrostis alba* and *Phalaris arundinacea* in northern Ohio, Evans and Ely (1935) stated that both rhizomes and above-ground shoots developed, to a limited extent, at all times when the weather conditions were favourable for growth. New rhizomes appeared in greatest numbers chiefly during June, July, August and early September. New above-ground shoots developed in the greatest numbers from August or September until the close of the growing season and during April and early May.

In Missouri, both Brown, E.M. (1943) and Etter (1951) noted that new rhizomes were produced by *Poa pratensis* in late spring and early summer. Most of these new rhizomes were observed by Etter to produce aerial shoots by late August. From Brown it would appear that the old rhizomes died during the summer. The production of new rhizomes was also noted by Etter to occur in late August, late September and early October; most of these formed aerial shoots before the winter. A lesser number of rhizomes was also noted by Etter to be formed at most other periods of the year.

The weight of rhizomes of *Agropyron repens* was measured by Arny (1932), in Minnesota, from May to November. During May the weight decreased slightly, increased during June but decreased again during the first half of July. From then until the beginning of October there was a relatively large increase, after which no distinct trend could be observed.

Corms and Bulbs

Of the grass species which develop corms or bulbs, *Phleum pratense* has been the most studied. In this species, the lower stem internode becomes enlarged to form a corm, which is frequently termed the haplocorm. Waters (1915), in Missouri, stated that a seed developed into a plant which in the spring produced a single stalk and flower-head. A haplocorm developed at the base of the stalk and enlarged as the stalk increased in height. About the time the seed-head appeared new shoots grew out from the haplocorm and developed

into young plants with independent root systems, most of this growth taking place at the expense of the parent haplocorm. The parent haplocorm reached its full development about the time the seed-head was ripe. The secondary plants continued to grow, and, under favourable conditions, produced seed-heads, while the parent haplocorm shrivelled and died. The young plants produced well-developed haplocorms before winter; in spring these sent forth stalks and repeated the cycle of the previous season.

Describing the life history of this species in Ohio and Washington, Evans, M. W. (1927) did not mention secondary growth but stated that the haplocorms were formed from about April until June and that most of them retained their form until next spring, although their interior parts were brown, non-turgid and apparently contained no living tissue. In New Jersey, Knoblauch, Ahlgren and Gausman (1955) stated that the corm weight per unit area of a sward was approximately 50% greater at the 'beginning bloom' stage in July than at the 'early heading' stage in June.

Roberts and Hunt (1936), in Wales, found that during the first year's growth of *Phleum pratense* plants the weight of root reached a maximum before that of the shoot. as it did in *Lolium perenne*, but, thereafter, the root-weight remained constant, not decreasing as it did in the latter species. No mention is made of haplocorms, which, if they were formed, were presumably classed as shoots. Roberts and Hunt concluded that the roots of *Phleum pratense* do not act as storage organs, as do the roots of *Lolium perenne*.

In Russia, Čepikova (1942) followed the life of haplocorms formed the previous year from 20th April until 5th June, i.e. from the beginning of shoot growth until the inflorescences emerged. Similar changes took place in the haplocorms to those which took place in the roots of *Festuca pratensis*. As the season advanced, the haplocorms became smaller and darker, the colloids of the living tissue decreased in volume and the enzyme catalase became less active, the haplocorm finally dying when the inflorescences were emerging and photosynthesis was at its maximum (see p. 33).

CHAPTER 8

LENGTH OF LIFE OF A NODAL ROOT

An adequate technique has not yet been devised to enable a functional root to be distinguished from a root which is of no value to the plant, i.e. non-functional and presumably dead. The criterion commonly used has been the decay of the root, but caution is needed in the use of this criterion as the cortex of a root may decay, leaving a functional stele. Again, a root may remain undecayed long after it has become non-functional. The capacity for imbibition by the colloids and the activity of the enzyme catalase in the root were criteria used by Čepikova (1942) while Goedewaagen (1955 personal communication), and Schwass and Jacques (in press) have used vital stains. The only conclusions which it is possible to draw from the few investigations reported are that the length of root-life varies between roots of the same plant and between plants of different species; it is also influenced by environment.

Stuckey (1941) divided the species that she studied into those with 'annual' and those with 'perennial' roots (Table 13). If all the roots were regenerated each year, the old roots disintegrating shortly after the new ones became established, the root system was considered 'annual'. Whenever the maximum production of roots occurred during the first year and these roots, for the most part, remained functional for more than one year, the root system was designated 'perennial'. In these latter root-systems there was some growth during the second autumn and spring, but the amount of new growth and decay was very small compared with the original root-growth during the first autumn and spring, and with the number of new roots produced by those species with 'annual' roots.

TABLE 13

Classification of root systems

(*Stuckey*, 1941)

Annual.	Perennial.
Phleum pratense.	*Poa pratensis.*
Agrostis alba.	*Poa compressa.*
Festuca elatior.	*Dactylis glomerata.*
Poa trivialis.	*Agropyron cristatum.*
Lolium perenne.	
Agrostis tenuis (probably).	

Stoddart (1935) and later Weaver and Zink (1946b) followed the life of individual roots by banding them with small pieces of metal (Table 14). Their results showed that the length of life of roots of the same species was not uniform, and that considerable differences existed between species. Weaver and Zink pointed out that the loss of roots developed during the first spring was considerable during the third season, i.e. second harvest year, but that, in proportion to the total number of roots developed by that time, it was very small.

Lolium italicum was noted by Schwass and Jacques (in press), working in New Zealand, to replace a greater proportion of its roots each year than either *Lolium perenne* or *Festuca arundinacea.*

TABLE 14

Percentage survival of banded roots at each examination.
Seeds sown and roots banded spring 1943

(*Weaver and Zink*, 1946b)

Species	Autumn 1943	Spring 1944	Autumn 1944	Spring 1945	Autumn 1945
Andropogon furcatus	100		100		81
Elymus canadensis		77		27	0
Panicum virgatum	100		100		
Agropyron smithii		64	42		
Andropogon scoparius	100		95	69	10
Bouteloua curtipendula		100		36	14
Stipa spartea	82		50		10
Bouteloua gracilis	100			66	45
Agropyron cristatum	97	75			
Bromus inermis	92	84	36		

An earlier deterioration of the cortex of the roots of *Lolium italicum* was also noted.

Several workers have mentioned the length of life of roots incidentally when dealing with other matters. Jefferies (1916) stated that the roots of *Molinia caerulea* functioned for three years, after which the cortex degenerated. Both Pavlychenko (1942) and Stevenson and White (1941) noted that the roots of *Agropyron pauciflorum* were short-lived, a high proportion probably dying each year. At least half of the root systems of *Poa pratensis* and of *Agrostis tenuis* were thought by Sprague, H. B. (1933) to be regenerated each spring (cf. Stuckey (1941)). In Russia, Skripčinskii (1955) noted that the new stems formed in the spring by plants of *Agropyron cristatum* were dependent upon the roots formed the previous year.

The length of life of a root was shown to be reduced by severe defoliation of the plant in an experiment by Weaver and Zink (1946b). A number of roots on seedling plants were banded and then half the plants had their shoot growth clipped back to 2″ above ground level every 10 days for 40 days. Of the banded roots of *Agropyron cristatum* 97% survived on the unclipped plants but 27% only on the clipped plants. The corresponding figures for *Bromus inermis* were 100% and 85%. An experiment with sods of *Andropogon furcatus* and *Andropogon scoparius* gave similar results.

CHAPTER 9

AGE OF THE PLANT

The root system of a grass plant is almost continually growing and the roots frequently live for more than one year (p. 36). Also, old roots are very slow to decompose (p. 123), so it is not surprising that the weight of roots under a sward was found by several investigators to increase with the age of the sward (Table 16). The relative amounts by which this weight increased varied with the environment and species. This increase in root weight usually resulted in a decrease in the weight of shoot produced per unit-weight of root after the first one or two years.

The time of most rapid root-growth apparently varied in different investigations. Brown, E. M. (1943) stated that swards of *Poa pratensis*, in Missouri, made much more rapid root-growth during the first six months after germination of the seed than at any subsequent period. Working with spaced plants, Pavlychenko (1942) found that the number and length of roots of three species (*Agropyron cristatum*, *A. pauciflorum* and *Bromus inermis*) increased to a far greater extent during the second year than in the first.

The weight of roots under a sward of *Poa pratensis* was found by Brown, E. M. (1943) not to vary with the age of the sward, although the weight of rhizomes increased with age. The more lenient the defoliation treatment, the greater was the increase (Table 15). If the plants received water during the period of summer drought, the weight of rhizomes decreased and the growth of the herbage increased. Brown was of the opinion that watering increased the rate of decay of the old roots.

The root-weight of plants of three species growing in containers was found by Weaver and Zink (1946a) to increase from the first to the second year, but to decrease from the second to the third year in the case of two species (*Bouteloua gracilis* and *Andropogon furcatus*) and to increase in another species (*Andropogon scoparius*). The same workers (1946b) counted the number of roots possessed by plants of ten American species of different ages, growing in containers, and found that in general the number increased with the age of the plant, but that some reached a maximum sooner than others.

Working with swards in England, Williams (1955) found that the greatest quantity of root material was produced in the first two years by early and quick establishing species such as *Lolium perenne*, *Dactylis glomerata*, *Festuca pratensis* and *Phleum pratense*, but in later years the root weight under swards of slower developing species such as *Agrostis tenuis*, *Festuca rubra* and *Poa pratensis* became just as great. This may be due to differences in the rate of growth or of decay.

TABLE 15

Relative dry weights of the roots and rhizomes of swards of *Poa pratensis* in successive years (*Brown, E. M.*, 1943)

Age (years)	Roots			Rhizomes		
	Cut semi-monthly 1″ high	Cut semi-monthly 2·5″ high	Hay cut	Cut semi-monthly 1″ high	Cut semi-monthly 2·5″ high	Hay cut
			Unwatered			
1	10	10	10	10	10	10
2	10	10	11	31	39	47
3	10	11	12	33	42	47
4	10	10	13	54	67	100
			Watered			
1	10	10		10	10	
2	12	12		9	9	
3	9	8		3	3	
4	10	7		5	3	

TABLE 16

Increase in the root weight of swards with age.
Relative dry weight of roots per unit volume of soil.
(Figures calculated to nearest unit)

Authority	Species	Depth of sample (inches)	Age of sward in years												
			1	2	3	4	5	6	7	8	9	10	12	15	Over 20
Nad'jarnyi (1939)	*Bromus inermis*	15·7	10	12	18										
Guščin (1940)	*Agropyron cristatum*	16	10	32	38	44									
	Agropyron desertorum		10	26	41	47									
Pavlychenko (1942)	*Agropyron cristatum*	12		10		21									
	„ *pauciflorum*			10		10									
	Bromus inermis			10		13									
Stevenson and White (1941)	*Agropyron cristatum*	12	10	15	20	23	28	27	31	30					
	„ *pauciflorum*		10	14	16	18	20					30			
	Bromus inermis		10	12	15	14	16								
Bates (1948)	Mixed	4	10	26	47	41	62								
				10	15	15	15	24							
				10	11	24	20	27	31						
Goedewaagen and Schuurman (1950a)	Mixed	7·9			10				9				12	11	11

When a sward is ecologically stable, an equilibrium must be maintained between growth and decomposition. The period taken from the time the seed is sown until this state of affairs is reached will vary with the species and environment. In the Belgian Congo, Bartholomew, Meyer and Laudelout (1953) have reported that a 'grass fallow' will attain this equilibrium in 2–4 years. This is probably a reflection of the favourable conditions for decomposition prevailing in the tropics; under more temperate conditions it is possible that equilibrium is not reached in such a short time.

Under field conditions, the percentage of the root-weight in the upper layers of the soil has been thought, by certain workers, to increase with the age of the sward, but this was not so in every investigation (p. 43).

CHAPTER 10

DISTRIBUTION OF ROOTS IN THE SOIL

Vertical Distribution

The depth to which the roots of a grass plant penetrate increases rapidly during seedling growth; thereafter the rate of penetration decreases. The maximum depth of penetration is not usually reached during the first year, although it is approached very closely.

The growth of twelve species of range grasses was studied by Plummer (1943) in Utah (Table 17). The depth of penetration did not increase as rapidly as did the total length or number of the roots. While differences in penetration and lateral spread were apparent between certain species, they were not as great as the differences in total root length. In general, the species with the greater total root length showed a deeper penetration and a wider spread.

The rate of increase in depth of root penetration by plants of four species was found by Kauter (1933) to become slower after the first 3 months' growth, although none reached their maximum depth during the first year. Deeper rooting and heavier root-weight were exhibited by the two 'early' species (*Lolium italicum* and *Arrhenatherum elatius*) than by the two 'late' species (*Festuca pratensis* and *Phleum pratense*), especially during the first year of growth. Working with seven species, including three which had been studied by Kauter, Könekamp (1934) measured the depth of penetration attained at intervals during the first 5 months' growth. The following year, the plants of three shallow-rooting species were observed for further penetration, but little further depth was attained. Similarly, Witte (1929) found, in four species, that the depths reached by the roots after 6 months' growth was not much less than those reached after 18 months' growth. Salonen (1949) also stated that the depth of rooting of *Phleum pratense* increased only slightly from the first to the third year. Villares, Tundisi and Becker (1953) concluded that age of a pasture had little effect upon the maximum depth of root penetration into the soil.

The depth of rooting of spaced plants was shown by Pavlychenko (1942) to be much greater than that of plants grown in a sward, i.e. grown in competition with each other. This was the case even after 4 years' growth.

The roots of grass plants are not equally distributed throughout the whole depth of penetration, but tend to concentrate in the upper layers of the soil. The actual distribution is, however, influenced by many factors. The distribution of

TABLE 17

Root growth of ten grass species as measured by vertical penetration and lateral spread per plant (*Plummer*, 1943)

Date	*Agropyron cristatum*	*Elymus glaucus*	*Arrhenatherum elatius*	*Agropyron spicatum*	*Bromus carinatus*	*Agropyron smithii*	*Festuca ovina*	*Elymus triticoides simplex*	*Stipa arida*	*Poa bulbosa*
					Root penetration (cm.)					
April 5	5	7	6	4	0	0	0	6	0	4
,, 12	6	7	7	6	0	0	0	8	0	4
,, 18	5	7	9	13	5	2	3	10	0	5
,, 25	10	13	10	14	9	4	4	10	1	6
May 2	12	15	16	17	15	5	5	10	5	8
,, 9	18	18	21	29	28	11	6	16	9	12
June 6	45	47	29	54	33	26	12	28	19	0
					Root spread (cm.)					
April 5	1	2	3	1	0	0	0	0	0	2
,, 12	1	3	3	1	0	0	0	1	0	2
,, 18	2	4	4	3	1	1	0	1	0	3
,, 25	4	5	4	4	4	1	1	2	0	7
May 2	5	8	9	9	6	1	2	3	0	6
,, 9	10	9	12	9	17	3	2	7	1	9
June 6	22	30	21	24	20	15	10	11	2	0

the roots of a 4-month-old *Lolium perenne* plant was exhaustively studied by Rappaport (1938) (Table 18). The maximum weight of roots occurred in the uppermost 5 cm., but the greatest total root-length and number of roots occurred at a lower depth. The concentration of weight in the upper layer was presumably due to the thick main roots.

TABLE 18

Root system of a 4-month-old plant of *Lolium perenne* grown without competition

(*Rappaport*, 1938)

Depth (cm.)	Dry wt. (mgr.)	Number of Main roots	Number of Branch roots	Number of Total	Length of Main roots (mm.)	Length of Branch roots (mm.)	Length of Total (mm.)
0–5	110	40	206	246	2335	3510	5845
5–10	70	27	253	280	850	7914	8764
10–15	50	18	337	355	790	7383	8173
15–20	45	15	224	239	730	6896	7626
20–25	32	14	186	200	660	4862	5522
25–30	30	11	161	172	550	3692	4242
30–35	18	10	173	183	500	2918	3418
35–40	14	9	117	126	450	1726	2176
40–45	10	9	46	55	420	740	1160
45–50	6	7	33	40	285	554	839
50–55	1	4	9	13	145	126	271
Totals	386	164	1845	2009	7715	40321	48036

TABLE 19

Percentage of roots as measured by dry weight in 10-cm. soil layers under several swards

(*Klapp*, 1943)

Dominant species	Soil layers of depth (cm.) 0–10	10–20	20–30	30–40	40–50
Reseeding 6–7 years previously with *Lolium perenne*, *Poa pratensis*, *Festuca rubra* and *Trifolium repens*					
Lolium perenne	80·3	9·3	4·6	3·5	2·3
Poa pratensis	61·8	28·7	4·5	4·0	1·0
Lolium/Poa	77·4	15·8	2·3	3·1	1·4
Trifolium repens	82·4	5·9	8·1	2·6	1·0
Heavily grazed pasture developed from heath by manuring					
Holcus lanatus	50·7	15·8	18·3	10·8	4·4
Agrostis vulgaris	59·0	25·3	9·0	5·2	1·5
Festuca rubra	73·5	12·8	4·6	3·6	5·5
Dactylis glomerata	52·5	29·8	13·3	4·4	—
Cynosurus cristatus	64·0	19·5	7·7	4·9	3·9
Poa trivialis	82·6	9·0	5·1	1·8	1·5
Mountain heath sward (*Calluna/Antennaria* association) moderately grazed					
Calluna	81·0	10·3	3·9	3·2	1·6
Nardus	71·2	13·6	6·9	5·6	2·4
Anthoxanthum/Festuca ovina	66·8	17·3	9·1	4·4	2·4
Holcus mollis	82·6	9·8	4·5	1·8	1·3
Boggy areas in the same localities only rarely grazed					
Deschampsia caespitosa	70·0	14·8	7·1	5·9	2·2
Lotus uliginosus	94·5	3·6	1·5	0·4	—
Park sward containing *Lolium perenne* and *Cynosurus cristatus*	83·8	8·8	5·9	1·5	—
5-year-old park sowings					
Dactylis glomerata	58·2	21·2	12·0	5·3	3·3

Results showing the concentration of roots in the upper layers of soil when measured by weight have been reported by numerous workers, e.g. Klapp (1943) in Germany (Table 19), Goedewaagen and Schuurman (1950a) in the Netherlands (Table 20), Troughton (1951) in Wales, Pavlychenko (1942) and Stevenson and White (1941) in Canada, Sprague, H. B. (1933) in New Jersey, Weaver and Zink (1946a) in Nebraska, Villares, Tundisi and Becker (1953) and Ampson (1954) in South America, Coetzee, Page and Meredith (1946) in South Africa, and Haworth (1953) in Ceylon. Considerable variation is apparent between the figures of the various workers, due, no doubt, to the different species studied and the different environmental conditions encountered.

TABLE 20

Variation in the air-dry weight of roots in grassland (q. per ha.) with age

(*Goedewaagen and Schuurman*, 1950a)

	Age of sward in years				
	3	7	12	15	Older than 20
Roots in layer 0–5 cm.	57	58	85	70	77
,, ,, ,, 0–20 cm.	89	78	109	100	98
,, ,, ,, 0–5 cm. as % of those in 0–20 cm.	64	75	78	70	78

It is possible, in some species at least, that the portions of older roots in the upper layers of the soil i.e. near the crowns of the plants, are not important for the absorption of water and nutrients from the soil. Goedewaagen (1955, personal communication), as a result of experiments employing the 'bleeding' technique (p. 133), was of the opinion that most of the water and nutrients are absorbed by the root-tip and to a lesser extent by those parts of the root upon which the cortex remains, and Schwass and Jacques (in press) have observed roots of *Lolium perenne, L. italicum* and *Festuca arundinacea* with the cortex missing for several inches proximal to the crown (p. 8).

Certain workers have reported that the concentration of roots in the upper layers of the soil increases with the age of a sward. Salonen (1949), stated that the root systems of pastures in Finland tended to accumulate close to the surface, a tendency which was more noticeable in old pastures than in young ones. The same tendency for roots to concentrate in the upper soil layers, as measured by weight, was noted by Goedewaagen and Schuurman (1950a) in leys under Dutch conditions (Table 20). This, they suggested, was due to the frequent defoliation of the leys by repeated cutting or grazing. The results of Pavlychenko (1942) with swards of *Bromus inermis*, *Agropyron cristatum* and *Agropyron pauciflorum* show that the concentration of roots in the upper layers increased with age; the results of Stevenson and White (1941) with the same species grown in rows also show this same general tendency although in their experiment it was not constant. In an experiment by Weaver and Zink (1946a) with individual plants which were defoliated once per year, no increase in the percentage of roots in the upper four inches occurred between the first and third years, but there was a decrease in the concentration in the lowest layer (24–34″). The percentage of the roots of a sward of *Agropyron* sp. in the upper 10 cm. was shown by Guščin (1940) to be higher in the first than in subsequent years. Increasing concentration in the upper layers is thus not a consistent feature of every experiment but it is not possible to distinguish, from the data available, the factors responsible for this variation.

The distribution of roots is also influenced by environmental factors, e.g. soil physical conditions, surface application of fertilizers. It is also influenced by defoliation. The influence of these factors is discussed in the sections devoted to them.

The value of deep roots to a plant during dry weather was shown by the work of Jacques (1941) and Laude (1953) (p. 75). Other authors have also emphasised their value, although often with little experimental evidence in support. Klapp (1943) and Schuurman (1954) were of the opinion that the susceptibility of a species to drought was often connected with a lack of roots in the lower depths of the soil, while Witte (1929) and Smelov and Ljubskaja (1940) stated that plants best able to grow in dry soils were those with deeply penetrating root systems. These deep roots are of value to a plant only while reserves of water exist in the lower layers of the soil. Once this water is exhausted, then the plants which are best adapted to utilize all the available surface moisture are those which are able to survive (p. 74 *et seq.*).

Under conditions when water is not in short supply, deep roots may not be of importance in the conduction of water. From a consideration of

TABLE 21

Depth of rooting (in inches)

Authors	Beckwith (1886)	Weaver (1926)		Witte (1929)	Kauter (1933)	Landbouwkundig Maandschrift (1935)	Linkola and Tiirikka (1936)			Smelov & Ljubskaja (1940)	Burton (1943)	Kübler (1954)	Haworth (1952)
Description or age of plants	Young	Tall Grass Prairie	Short Grass Plains	18 months	1 year	4 months	*Antennaria* Meadow	*Nardus* Meadow	*Alchemilla* Meadow	1st year	9 months	?	3 years
Location	New York	Nebraska		Bonn	Zürich	Netherlands	Finland			Russia	Georgia	Germany	Ceylon
Species													
Agropyron repens	—	—	—	63	—	—	—	—	—	—	—	—	—
Agrostis alba	—	—	—	47	—	—	—	—	—	—	—	—	—
,, *canina*	24	—	—	—	—	—	—	—	—	—	—	—	—
,, *capillaris*	—	—	—	—	—	—	18–24	3–5	3–5	—	—	—	—
,, *stolonifera*	—	—	—	—	—	20	—	—	—	—	—	—	—
,, *vulgaris*	40	—	—	—	—	—	—	—	—	—	—	—	—
Alopecurus pratensis	34	—	—	39·5	—	—	—	—	—	39·5	—	41	—
Andropogon furcatus	—	108	—	—	—	—	—	—	—	—	—	—	—
,, *nutans*	—	36–66	—	—	—	—	—	—	—	-	—	—	—
,, *scoparius*	—	36–66	—	—	—	—	—	—	-	—	—	—	—
Anthoxanthum odoratum	—	—	—	39·5	—	—	3–5	1–3	1–3	—	—	—	—
Arrhenatherum elatius	—	—	—	110	60	—	—	—	—	—	—	73	—
Avena elatior	24	—	—	—	—	—	-	—	—	—	—	—	—
Axonopus affinis	—	—	—	—	—	—	—	—	—	—	32-36	—	—
Bouteloua gracilis	—	—	48	—	—	—	—	—	—	—	—	—	—
,, *hirsuta*	—	—	24–42	—	—	—	—	—	—	—	—	—	—
Bromus inermis	—	—	—	86·5	—	—	—	—	—	78·5	—	—	—
,, *mollis*	—	—	—	—	—	—	—	—	—	—	—	14	—
Bulbilis dactyloides	—	—	24–36	—	—	—	—	—	—	—	—	—	—
Cynosurus cristatus	—	—	—	15·5	—	12	—	—	—	—	—	—	—
Dactylis glomerata	—	—	—	39·5	—	—	—	—	—	39·5	—	63	—
Digitaria eriantha	—	—	—	—	—	—	—	—	—	—	36 40	—	—
Deschampsia caespitosa	—	—	—	47	—	—	—	—	24–32	—	—	—	—
Deschampsia flexuosa	—	—	—	—	—	—	24–32	18–24	5–12	—	—	—	—
Elymus canadensis	—	24–36	—	—	—	—	—	—	—	—	—	—	—
Festuca elatior	32	—	—	—	—	—	—	—	—	—	—	—	—
,, *ovina*	27	—	—	23·5	—	16	24–32	3–5	1–3	—	—	—	—
,, *pratensis*	—	—	—	39·5	42	—	—	—	—	63	—	37	—
,, *rubra*	—	—	—	47	—	16	24–32	3–5	3–5	49	—	—	—
Holcus lanatus	—	—	—	55	—	—	—	—	—	—	—	—	—
Koeleria cristata	—	18–24	—	—	—	—	—	—	—	—	—	—	—
Lolium italicum	—	—	—	—	49·5	—	—	—	—	—	—	—	—
,, *perenne*	—	—	—	39·5	—	23	—	—	—	57	—	29	—
Muehlenbergia gracillima	—	—	24	—	—	—	—	—	—	-	—	—	—
Nardus stricta	—	—	—	—	—	—	32–40	18–24	24-32	—	—	—	—
Panicum virgatum	—	96–108	—	—	—	—	—	—	—	—	—	—	—
Paspalum species	—	—	—	—	—	—	—	—	—	—	36–40	—	—
Phalaris arundinacea	33	—	—	110	—	—	—	—	—	—	—	—	—
Phleum pratense	34	—	—	31·5	41	—	—	—	—	—	—	47	—
Poa nemoralis	—	—	—	—	—	16	—	—	—	—	—	—	—
Poa pratensis	—	—	—	39·5	—	11	—	—	—	49	—	18	—
Poa trivialis	—	—	—	—	—	12	—	—	—	—	—	10	—
Spartina michauxiana	—	96–132	—	—	—	—	—	—	—	-	—	10	—
Stipa spartea	—	24–36	—	—	—	—	—	—	—	—	—	10	—
Tripsacum laxum	—	—	—	—	—	—	—	—	—	—	—	—	120
Trisetum flavescens	—	—	—	23·5	—	—	—	—	—	—	—	23	—

theoretical factors, Wind (1955) was of the opinion that, when the water-table was 50 cm. from the surface, the pressure gradient required for water to flow through the roots of *Lolium perenne*, *Dactylis glomerata* and *Phleum pratense* at a depth below 10–20 cm. was greater than the gradient required for the water to flow through the soil by capillary, so that the passage of water through the roots at these depths was negligible compared with that through the soil.

Several workers have compared plants of different species on the basis of the depths penetrated by their roots. The plants were, of course, grown in the same environment. Some of these results are summarised in Table 21. Considerable variation is apparent between the species and environments.

Other workers have used the distribution of the roots as the basis for their comparisons between species, usually measuring the roots by weighing them, e.g. Klapp (1943) (Table 19) and Baumann & Klauss (1955) in Germany, Schuurman (1954) in the Netherlands, Pavlychenko (1942), Stevenson and White (1941) in Canada, and Partridge (1941), Burton (1943), Gist and Smith (1948), Lamba, Ahlgren and Muckenhirn (1949) and Hopkins (1953) in America. Torstensson (1938) and Sprague, H. B. (1933) have compared the root distribution of more than one species when subjected to varying degrees of defoliation (pp. 98–9).

Visual observation has also been used to compare the distribution of roots, e.g. Beckwith (1886) and Weaver (1926) in America, and Murray and Glover (1935) in South Africa. Another criterion used was that of Witte (1929) who counted the numbers of roots at descending intervals (Table 22).

Könekamp (1934) classified species according to the rate of penetration of their roots during seedling growth. This classification was substantiated at the end of the growth period by the distribution of the roots by weight, those species which penetrated quickest having a high percentage of their root-weight in the lower layers of the soil.

A difference between grasses on the basis of the vertical distribution of their roots was suggested by Baumann and Klauss (1955). In an experiment carried out in pots with a water-table at a depth of 36 cm. they found that cultivated grasses (those used in seeds mixtures) had a high proportion, on average 67%, of their roots in the 0–12 cm. layer of soil; grasses which are constituents of permanent pastures, (but which, on account of low yields are not used in seeds mixtures) had, on average, less than half their root mass in the 0–12 cm. layer. Grasses which live as weeds of arable land had the highest percentage (75%) of root growth in the 0–12 cm. layer.

Horizontal Distribution

Little work has been carried out on the horizontal distribution of roots and little is known of the factors that influence it. It would be expected that the roots of a plant grown in a sward would have less lateral spread than those from plants grown alone.

Beckwith (1886) and Plummer (1943) both measured the lateral root-spread of seedlings of several grass species (Table 17). The species with roots which penetrated to a great depth were generally those with a wide lateral spread of roots. Weaver (1926) and Linkola and Tiirikka (1936) (Table 23) measured the lateral spread of roots of more mature plants. The latter workers showed that the lateral spread does vary to some extent with the environment.

Protected plants of *Agropyron inerme* in Utah were shown by Hanson and Stoddart (1940) to have root systems with a lateral spread of 40 cm., while grazed ones had a spread of 46 cm. This increase is at variance with the trend shown by the depth of penetration and the weight of roots per unit volume. Hanson and Stoddart studied only a few plants and their results may be unreliable.

TABLE 22

Number of roots per 1298 square centimetres

(*Witte*, 1929)

Depth (in cm.):—	10		20		40		60		80		100		120		140		160		180		200		220		240		260		280	
Species	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Phalaris arundinacea	2766	520	2257	343	1045	208	816	224	754	203	588	192	593	172	416	161	447	120	452	120	68	5	99	5	21	1	10	0	5	0
Arrhenatherum elatius	5320	619	4129	499	1534	244	822	192	712	172	520	99	328	52	437	135	281	31	312	47	151	5	42	5	21	0	5	0	3	0
Bromus inermis	6214	806	3723	437	1706	380	900	276	525	161	322	78	260	36	135	10	125	10	244	5	73	5	3	0	—	—	—	—	—	—
Agropyron repens	1622	140	749	68	291	52	276	36	192	21	109	16	99	5	10	0	5	0	—	—	—	—	—	—	—	—	—	—	—	—
Holcus lanatus	2257	515	1300	104	567	57	541	42	382	26	146	26	42	16	47	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Aira caespitosa	not counted		957	229	629	135	255	42	182	36	62	0	10	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Festuca rubra	6027	447	2662	172	952	120	468	36	234	10	156	10	21	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Agrostis alba	not counted		3453	182	1004	78	541	57	192	10	203	10	36	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dactylis glomerata	7722	156	4082	99	1269	78	764	36	156	0	36	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Alopecurus pratensis	5247	645	3848	364	1222	104	473	47	317	36	26	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Poa pratensis	not counted		1310	177	650	73	260	52	224	47	104	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Anthoxanthum odoratum	not counted		322	78	21	10	21	0	1	0	1	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lolium perenne	not counted		1706	146	208	68	161	52	57	16	26	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Festuca pratensis	4009	281	2252	135	744	62	198	31	62	5	6	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Phleum pratense	5070	463	2766	130	572	47	47	0	16	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Festuca ovina	not counted		1763	218	1030	88	203	26	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Avena flavescens	not counted		1269	88	177	26	5	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cynosurus cristatus	not counted		858	42	104	0	—		—		—		—		—		—		—		—		—		—		—		—	

A = Total number of roots
B = Number of thick roots <0·2 mm. diameter

TABLE 23

Length and lateral spread of root systems of plants in 3 environments, in cm.

(*Linkola and Tiirikka*, 1936)

Species	Length of roots of the 1st order			Length of roots of the 2nd order			Breadth of root system		
	Antennaria pasture	*Nardus* pasture	*Alchemilla* pasture	*Antennaria* pasture	*Nardus* pasture	*Alchemilla* pasture	*Antennaria* pasture	*Nardus* pasture	*Alchemilla* pasture
Anthoxanthum odoratum	6–23	8–24	8–21	0·5–2·5	0·5 3	0–3	35	40	35
Agrostis capillaris	25–91	9–28	6–20	2–9	1–3	1–2	20–30	35–50	20–35
Deschampsia caespitosa	–	15–70	7–80	–	1–5	1–5	–	55–60	(50)
Deschampsia flexuosa	45–90	11–36	10–33	1–23	1–6	1–6	50	50	(50)
Festuca rubra	60–70	8–36	9–26	2·5–10	0·5–2	0·5–2	(25)	50–60	(50)
Festuca ovina	60–90	9–40	13–19	4–12	0·5–3·5	1–3	30–40	40–60	30–35
Nardus stricta superficial	3–17	8–28	7–34	0·5–2	1–6	1–6	30	55–60	50–60
deep	24–100	?–70	?–80	2–10			50		
Poa angustifolia	55–70	–	–	0·5–10	–	–	30	–	–

CHAPTER 11

GENETIC DIFFERENCES

Species Differences

Different species can be fully compared only by studying plants at all stages of their life-histories and while they are growing in all the environments in which they are able to live. This is rendered necessary because different species require different conditions for their optimum growth and all species do not react to the same extent to a change in environment.

As this ideal is not practical, investigators have compared the root systems of different species either by growing plants of each species under the same environmental conditions or by studying the root system produced by each species under a wide range of natural environments and then comparing the species on the basis of the 'mean' of all environments. The first procedure has been termed the 'specific environment' method and the second the 'survey' method. When using the specific environment method it is, of course, possible to compare the species under several environments in one investigation and then to compare the species using the 'mean' of all environments. By doing this, all the species are represented in all environments; in a survey all species may not be present in every environment.

To enable a complete comparison to be made, the plants should be examined at all stages of their life cycle but usually workers have only compared the plants on one date.

In certain investigations the same species have been compared in several environments which have differed from each other only in the amount present of a single factor necessary for growth, e.g. water, heat or in the treatment given to the herbage. In most of these investigations, interest has been centred on the effect of the growth factor or herbage treatment rather than on the species. This type of investigation has been carried out both in 'artificial' environments, e.g. greenhouses or growth chambers, and in 'natural' environments.

When plants are grown for comparison in the same environment, they may be grown either as spaced plants or in a sward, in the field or in containers, and in 'natural' or 'artificial' environments. The survey method is largely confined to plants grown under natural or agricultural conditions, and so has the disadvantage that in natural grasslands a species will tend to grow only where conditions approach the optimum for its growth, so that the range of conditions may be different for each species. Again, all the environments in which a particular species occurs may have a common factor which exerts a strong influence upon the root-system, e.g. a low soil pH which retards the decay of old roots. These disadvantages do not apply so much to sown grasslands where the final result may be the 'mean' of a wide range of conditions.

Weaver used the survey method extensively in his early work when he compared root systems by means of written descriptions and diagrams (1919, 1920, 1926) as did Coetzee, Page and Meredith (1946) in South Africa. Kmoch (1952) also used this method in Germany, not only for the comparison of species but to study the effect of various environmental influences such as the pH and the chemical composition of the soil. Relatively few other workers have used this method.

Most workers have used the weight of roots as their criterion of comparison e.g. Schuurman (1954), Troughton (1954), Baumann and Klauss (1955). A few workers have used other criteria; Witte (1929) used the number of roots to compare 18-month-old plants grown under one environment at Bonn (Table 22) while Linkola and Tiirikka (1936) used the lengths of main roots and their first-order branches (Table 23). Pavlychenko (1942) used both the weight and length of all orders of branches to compare 10 species grown in Nebraska (Table 2).

In the Appendix is presented a summary of the available data on the weight of roots under swards, on which basis most comparisons have been made. Similar data concerning single plants may be found throughout the text. It is not possible to draw any general conclusions from a comparison of species because of the many factors involved. The Appendix does, however, give some idea of the differences to be expected.

Strain Differences

The same principles apply to a comparison of the strains of one species as to a comparison of species. Most investigators, as when comparing species, have compared strains using the weight of roots produced in one environment as their criterion of comparison. Stevenson and White (1941) compared two strains of *Agropyron cristatum* each year for eight years, while Burton (1943) compared two strains of *Paspalum notatum* after 9 months' growth. Small differences were noted between the strains. The differences between strains of *Bromus inermis* of known drought resistance were studied by Cook (1943) (pp. 77–8). Jacques and Edmond (1952) compared the initiation of roots following root pruning of 'certified' and 'uncertified' *Lolium perenne* plants (pp. 103–4). The maximum depth of rooting of several strains of *Dactylis glomerata*, *Festuca pratensis*, *Arrhenatherum elatius* and *Bromus inermis* were compared by Witte (1929), as were two strains of *Agrostis stolonifera* in another experiment (*Landbouwkundig Maandschrift* 1935). Stapledon (1924), at Aberystwyth, was unable to find any difference in the reaction of indigenous and non-indigenous strains of *Dactylis glomerata* to defoliation treatments. In general, it appears that strains within a species vary in a similar manner to the species themselves, but normally not to such a great extent.

CHAPTER 12

CHEMICAL COMPOSITION

The chemical constituents of a plant may be conveniently divided into the carbohydrate, nitrogenous and mineral fractions (Table 24). The carbohydrate fraction is usually considered as being derived from the photosynthetic activity of the shoots, while the nitrogen and minerals are obtained from the growth media through absorption by the roots. It has been shown that the excised roots of many species are capable of

TABLE 24

The yield and composition of stubble and roots of 4-month-old *Lolium perenne* plants (expressed as percentage of dry weight except first and last items)

(*Sullivan and Sprague*, 1943)

Analysis	Stubble	Roots
Total yield of dry matter in grams per pot	4·09	6·78
Total constituents accounted for	80·23	79·18
Dry matter soluble in alcohol	21·16	13·53
Fructose	1·79	0·88
Glucose	2·01	0·29
Sucrose	6·08	2·89
Fructosan	15·04	1·81
Aldose obtained from oxalic acid hydrolysis as glucose	0·75	0·34
Pentosan as xylose	16·21	24·53
Fermentable aldoses from sulphuric acid hydrolysis as glucose	4·35	2·02
Cellulose	27·37	32·00
Lignin	3·99	12·23
Alcohol-soluble N	0·20	0·08
Alcohol-insoluble N	0·97	0·95
Total N	1·17	1·03
Alcohol-soluble N in percentage of total N	16·81	8·15

absorbing carbohydrates from the growth media and utilising them for growth (Thomas, 1947) but it is not known how important this process is in whole plants under natural conditions. The quantity and concentration of a chemical constituent in a particular organ will vary with the absorption, photosynthetic, enzymatic and translocatory activities within the plant.

It is the 'reserve' as opposed to 'structural' materials which are subject to the greatest variations in concentration within a plant. According to Thomas (1947), before a substance can be classified as a reserve food it must be shown that a preliminary period of accumulation is followed by a period in which the substance is maintained *in situ* at a relatively high concentration, and that later, in association with physiological processes taking place in the immediate vicinity or elsewhere, the concentration diminishes. The most important reserve substances of grasses were considered by Weinmann (1948a) to be certain groups of carbohydrates, viz. sugars, fructosans, dextrins and starch. The more complex carbohydrates, such as pentosans, hemicellulose and true cellulose, he considered to be structural materials which could not be further utilised by the plant. These conclusions were reached as a result of a study of the seasonal variation and effect of defoliation. Similar opinions were held by McCarty (1938), Brown, E. M. (1943) and Sullivan and Sprague (1953).

Other workers, however, have been of the opinion that hemicellulose may act as a reserve substance. This view was taken by Leukel and Coleman (1930) as a result of their work on the chemical composition of *Paspalum notatum*, and by Morosov (1939) as a result of work with three temperate species. Both Jefferies (1916) and Arber (1934), on anatomical evidence, stated that cellulose acted as a reserve in *Molinia caerulea*. McCarty (1938) thought that it was possible that the hemicellulose in the roots of *Bromus carinatus* was converted into simpler compounds, but that the rate of such conversion was very slow. If hemicellulose does act as a reserve substance, then its importance would appear to be small, as no worker appears to have noted large variations in its concentration.

Kirchner, Loew and Schröter (1908) were among the earliest workers to realise the importance of fructosans as reserve substances in certain grasses. The presence or absence of these compounds in their tissues has been used by De Cugnac (1931) to classify the members of the Gramineae into two major groups:

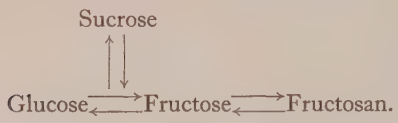
Group 1. 'Les saccharifères'. These grasses never form fructosans in their tissues, but contain sucrose, reducing sugars (glucose and fructose) and sometimes starch. This group could be subdivided on the basis of the presence or absence of starch.

Group 2. 'Les lévulifères', which are characterised by the presence of fructosan. Starch is

not formed in the grain and, while it may co-exist with the fructosans, its presence is purely transitional. This group could be sub-divided according as to whether or not the fructosan could be hydrolysed by sucrase.

In the first group, De Cugnac listed, amongst others, *Brachypodium pinnatum*, *Cynodon dactylon*, *Panicum stagninum*, *Sorghum halepense* and *Spartina polystachya*, and in the second group *Alopecurus agrestis*, *Agropyron repens*, *Agrostis alba*, *Arrhenatherum elatius*, *Dactylis glomerata*, *Festuca pratensis*, *Lolium perenne* and *Phleum pratense*. He suggested that the 'Graminées lévulifères' were essentially grasses native to cool temperate climates, while the 'Graminées saccharifères' were mostly adapted to warm climates.

A fructosan was found to be the major reserve substance in the haplocorms of *Phleum pratense* by Harper and Phillips (1943) who put forward the following scheme to account for the relationships between certain of the carbohydrate constituents:



The interconversion of glucose and fructose was assumed to be slower than the other reactions. Sucrose was apparently formed following the hydrolysis of the fructosan. Archbold (1940), in her review of fructosans in monocotyledons, noted that conditions which tend to promote sugar storage also result in the production of relatively large amounts of fructosan. Sullivan and Sprague (1943) considered that, owing to faulty analytical methods, fructosans were often incorrectly reported as dextrin and starch. The chemical structure and properties of the carbohydrates, mainly fructosans, found in the roots and rhizomes of *Agropyron repens* have been the subject of an intensive study by Arni and Percival (1951).

Several investigators have commented upon the importance of non-reducing sugars, especially sucrose, as reserve substances. Rapp (1947) concluded that in *Sorghum halepense* sucrose was a more important reserve substance than starch, dextrin or the reducing sugars. In *Stipa pulchra*, Sampson and McCarty (1930) thought that polysaccharides and sucrose were more important as accumulation products than the mono-saccharides. Non-reducing sugars were found by Weinmann and Reinhold (1946) to be the principal reserves in the majority of the 13 South African grasses which they studied. Sucrose was found by Morosov (1939) always to dominate the mono-saccharides in three temperate grasses.

Roots, rhizomes, corms and leaf bases all apparently act as storage organs, their relative importance varying with the species and possibly the environment. Reserves are also found, but to a much more limited extent, in other parts of the shoot system. In general, all parts of a plant have the same basic composition, but the concentration of a constituent may vary between different organs. Summarising their work on *Lolium perenne* and *Dactylis glomerata*, Sullivan and Sprague (1953) stated that the greatest accumulation of soluble carbohydrates (i.e. reserve carbohydrates) occurred in the lower parts of the leaf blades and sheaths (stubble) as a net result of a negative downward gradient of sucrose and a positive downward gradient of fructosans, the latter being the more abundant. A gradient was not evident for reducing sugars. In the roots, total soluble carbohydrates were lower than in the stubble on a percentage basis, but were sometimes larger on an absolute basis. Fructosan was usually the predominant reserve carbohydrate of the stubble and sucrose was often the predominant reserve in the roots. Baker, H. K. (1955) working with *Lolium perenne* also noted that the percentage of total soluble carbohydrates was always greater in the stubble than in the leaves or the roots. Sampson and McCarty (1930) likewise noted a higher concentration of reserve carbohydrate in the leaf bases of *Stipa pulchra* than in the roots, while Brown, E. M. (1943) in his studies with *Poa pratensis* found that the rhizomes always contained a higher percentage of sugars and starch than did the roots.

In studying changes in the composition of plants, the concentration (percentage) of a constituent, its absolute quantity, or both, may be determined. Most workers have studied concentrations only, as a comparison of absolute amounts usually involves the determination of the weight of roots as well as the concentration of the chemical constituent. The disadvantages of using concentration as the only criterion are obvious as the variations in the weight of the plant are not taken into consideration.

In addition to the more usual chemical constituents, the roots of certain grasses contain aromatic substances. Examples of such grasses are

Cymbopogon nardus, *Vetiveria zizanioides*, *Melica* sp., *Anthoxanthum odoratum* (Stapf, 1906; Arber, 1934).

Seasonal Variation of Carbohydrates in the Roots

The results of Klapp (1937a) show that during the growth of young plants (98 to 127 days old) of *Dactylis glomerata* and *Poa pratensis* the quantity of carbohydrates in the roots and the leaf bases (tillering zone) increased to a greater extent than did the quantity of total dry matter. This was particularly marked in the plants of *Dactylis glomerata*. As the plants became older (127 to 192 days) this trend became less marked.

When a plant is established, its growth is controlled, under natural conditions, by the seasonal cycle. In general, it seems that a grass plant stores carbohydrates in the roots etc. during the periods of slow herbage growth in spring, summer and especially autumn. These reserves are then used during periods of rapid herbage growth and for initial herbage growth in spring, as well as for respiration and growth during winter. If the plant is defoliated at any time, then reserves are utilised for the production of new photosynthetic tissue.

These general trends are shown in the results of McCarty and his co-workers with several range grasses in Utah. In general, they found that during the growing season, the storage of carbohydrates in the roots and stem bases was inversely related to herbage growth, i.e. high growth-rate, little storage; and vice versa. Growth, consisting of herbage and adventitious roots, made previous to the disappearance of snow and in early spring was found to consume approximately 70–75% of the sugar and starch accumulated during the previous autumn. Carbohydrate stores (i.e. sugar and starch) were lowest at the time of most active herbage growth, and storage was at its maximum during the autumn when herbage growth was complete. A minor decrease in stores of carbohydrates occurred at the time of secondary herbage growth and a progressive one during the winter, presumably due to respiration. The maximum concentration of hemicellulose prevailed during the formative stage of shoot development; low values coincided with the development of the seed and the storage of sugar and starch. There was some evidence that the sucrose increased at the expense of the starch during the period of low autumn temperatures. The combined percentages of starch and sugar in the herbage dropped at the time of most active growth and increased during flowering and seed formation. The percentage of hemicellulose rose at the beginning of the season and then remained more or less constant until the autumn.

The species studied in these investigations were *Stipa pulchra* (Sampson and McCarty, 1930), *Avena fatua* (McCarty, 1932), *Elymus ambiguus*, *Muehlenbergia gracilis* (McCarty, 1935), *Bromus carinatus* (McCarty, 1938) (Fig. 6) and *Agropyron trachycaulum* (McCarty and Price, 1942).

Similar variations were noted in some South African high-veld grasses (e.g. *Trachypogon plumosus*, *Tristachya hispida*, and *Digitaria tricholaenoides*) by Weinmann (1940a) and Weinmann and Reinhold (1946). The percentage of reserve carbohydrates (sugars and starch) in the roots increased during the autumn, reaching maximum values during mid-winter and decreased during spring and early summer. In the shoots, total sugars increased after flowering and declined during maturation, i.e. in autumn and early winter. It was concluded that carbohydrates were elaborated in the leaves in excess after flowering, and that they were subsequently translocated to the roots, where they were stored to be drawn upon in the following spring for the production of new shoot-growth.

The same general trend is ascertainable in the results of Brown, E. M. (1943) working with *Poa pratensis* in Missouri, but there are certain differences in the spring and summer which may be due to species, environment or to the regular partial defoliation which Brown's plants received. The plants used by McCarty and Weinmann were allowed to grow undisturbed. Brown measured both the concentration and absolute quantities of certain constituents in the roots and rhizomes and concluded that the period most favourable for storage was in the autumn after the growth of the herbage had practically ceased. In the early spring, carbohydrates were synthesised more rapidly than they were used, i.e. they were stored in the roots, while during the late spring and early summer the opposite occurred, i.e. carbohydrates were lost from the roots. Brown attributed this loss to the very high temperature at this time, as *Poa pratensis* is a cool-weather species, being particularly susceptible to high temperature. The hemicellulose content was considered by Brown

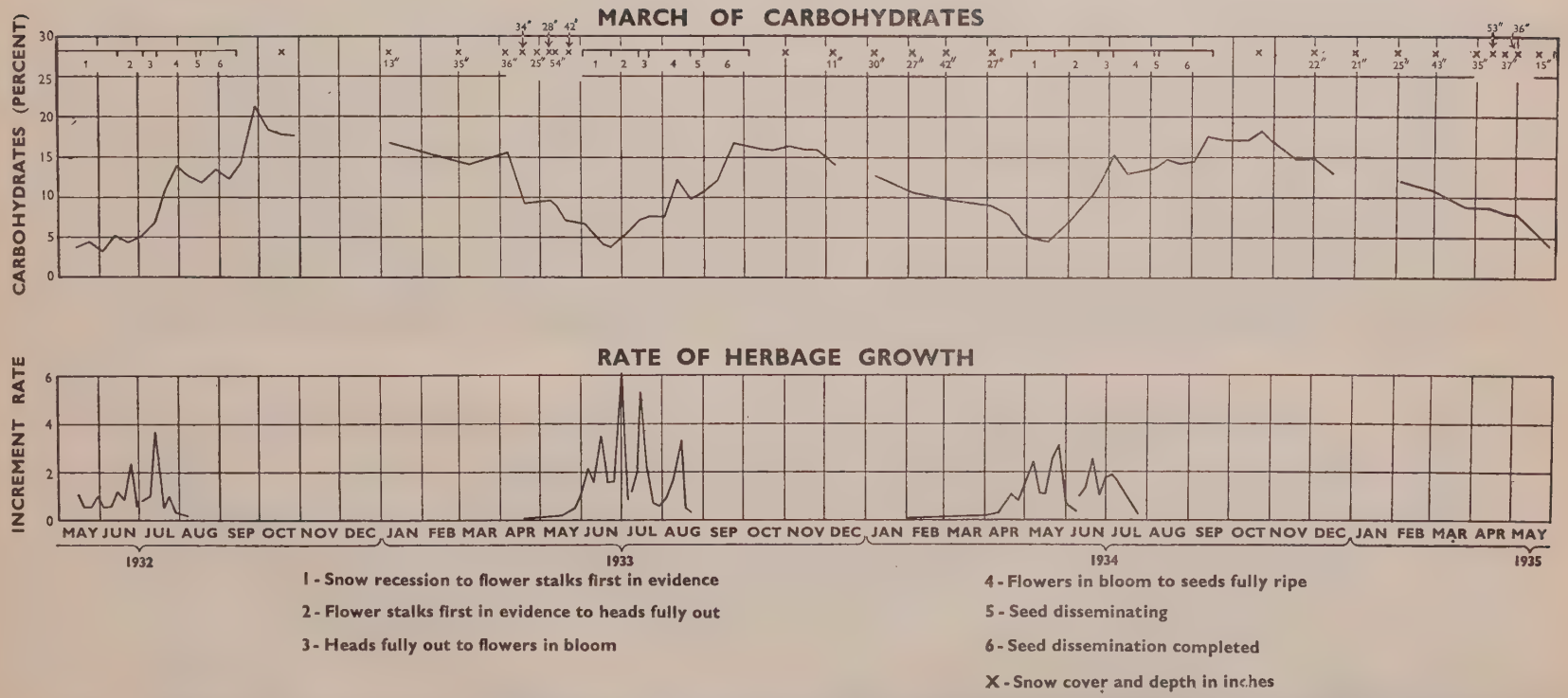

MARCH OF CARBOHYDRATES
CARBOHYDRATES (PERCENT)
30
25
20
15
10
5
0
RATE OF HERBAGE GROWTH
INCREMENT RATE
6
4
2
0
MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY
1932
1933
1934
1935
1 - Snow recession to flower stalks first in evidence
2 - Flower stalks first in evidence to heads fully out
3 - Heads fully out to flowers in bloom
4 - Flowers in bloom to seeds fully ripe
5 - Seed disseminating
6 - Seed dissemination completed
X - Snow cover and depth in inches

Fig. 6. The changes of the combined fractions, reducing sugars, sucrose and starch in roots and stem bases in relation to growth of *Bromus carinatus*. (*McCarty*, 1938)

to be unimportant as a reserve substance, as its concentration varied only slightly.

The general trend noted by McCarty and Weinmann in connection with herbage growth was found also by McIlvanie (1942) in *Agropyron spicatum*, and Aldous (1930) in *Andropogon scoparius*. The two latter workers both found a decrease in the concentration of reserve carbohydrates in the roots concurrent with early shoot growth and then a gradual increase during the late spring and summer followed by a decrease at the time of secondary herbage growth. McIlvanie stated that the greatest relative amounts of reducing sugars in the roots were associated with rapid vegetative growth; the greatest quantities of sucrose were associated with differentiation and the greatest quantities of 'reserve polysaccharide' with the brief rest period prior to secondary growth.

All investigations appear to indicate that carbohydrates are stored in the roots during the autumn. In addition to the work already mentioned, storage of carbohydrates in the autumn was also noted in *Digitaria eriantha*, by Bews and Bayer (1931), and by Arber (1934) in *Molinia caerulea* and *Poa bulbosa*.

As previously stated, the percentages of sugars and starch in the roots of *Bromus carinatus* were found by McCarty (1938) (Fig. 6) to increase in the autumn while that of the hemicellulose decreased. This led McCarty to suggest that the enzymatic transformation of the hemicellulose into simpler compounds took place, but Weinmann (1948a) thought that this inverse relationship was merely due to expressing the results as percentages. McCarty also found that during this period the concentration of sucrose increased at the expense of the starch, the maximum percentage of sucrose being reached before the first permanent snowfall of winter. This change McCarty attributed to the stimulation of enzymatic activity by low autumn temperatures. The increase in sucrose concentration resulted in an increased water-holding capacity on the part of the plant. This helped it to withstand the desiccating influence of the low relative humidity and the deficiency of soil moisture experienced before the first permanent snowfall, and was associated with resistance to low temperature and winter survival.

A decrease in the available carbohydrate content of the basal organs occurring concurrently with spring herbage growth has been noted by several workers. It was particularly noticeable in the results of McCarty in whose experimental plants the reserve carbohydrates were utilised for the growth of herbage and nodal roots prior to the disappearance of snow. In the case of *Bromus carinatus*, McCarty emphasised the fact that, although most (75%) of the starch and sugar accumulated during the previous autumn was utilised in the making of this growth, the herbage at the time of the minimum level of carbohydrates had reached only one-tenth of its maximum annual height. He therefore concluded that normal current growth and yield were independent of stored sugars and starches and were the products of carbohydrates concurrently manufactured in the shoot. McIlvanie (1942), however, found that *Agropyron spicatum* made approximately 45% of its current growth in height before the concentration of reserves in the roots ceased to decline.

Carbohydrate reserves are also utilised in the autumn for the production of new shoots (secondary herbage growth), although, in this instance, a smaller proportion of the reserves are utilised, e.g. in plants of *Bromus carinatus*, 15% of the reserves were utilised in the autumn as compared with 75% in the spring (McCarty, 1938).

Seasonal Variation of Carbohydrates in Corms, Bulbs, Rhizomes and Leaf Bases

The relative importance of these organs compared with the roots as storage organs appears to vary with the species and possibly with the environment. Certain of the major changes, e.g. loss of reserves at the time of the initial shoot growth, are apparently common to all the storage organs, but considerable variation was reported between them when other, less drastic changes occurred.

In the firm, young haplocorms of *Phleum pratense* grown in Missouri, the results of Trowbridge, Haigh and Moulton (1915) indicated that the quantity of 'nitrogen-free extract' increased rapidly from early spring until the plants began to head, and then more slowly until the plants reached the 'seed in dough stage'. The quantity then remained more or less constant until the seed was ripe. The quantity of 'crude fibre' increased rapidly until the plants were in full bloom and then remained more or less constant. Similar changes were shown in the quantity of 'ether extract', except that a temporary decrease

took place while the seed was being formed. These haplocorms later produced new shoots at the expense of their reserves. In more recent work with similar material grown in New Hampshire, Harper and Phillips (1943) found that the concentration of fructosan increased rapidly during June while the flowering heads were forming, after which it remained more or less constant until October when it declined slightly: it was unaffected by the flowering of the plant or by the secondary herbage growth. The percentages of glucose, fructose and sucrose varied considerably during this period but showed no distinct trends. Harper and Phillips put forward a scheme to explain the relationships between the various carbohydrates (p. 50). Over-wintering was found to result in a great decrease in the concentration of fructosan (from 47 to 29%) and slight increases in the percentage of the sugars. In Russia, Smelov (1937) found that the percentage of water-soluble carbohydrates and hemicellulose decreased gradually from the time the seeds on the 'mother' shoot ripened to the time the 'daughter' shoots were growing in the following year, i.e. from July to May. From these investigations it would appear that the haplocorm and its store of 'reserve' carbohydrate develop during the growth of the shoot. Some carbohydrate is lost throughout the winter and the remainder is utilised in the spring for shoot growth. The haplocorm then dies as the 'daughter' haplocorms grow.

The results of Brown, E. M. (1943) regarding the quantity of carbohydrates in the roots of *Poa pratensis* have already been described (pp. 51, 53). During the cool, early spring carbohydrates were synthesised more rapidly than they were utilised in the shoot and the balance was transferred to the rapidly-growing roots. Some loss of carbohydrates occurred in the rhizomes, however. During the hot weather of late spring and early summer there was a net loss of carbohydrates from the roots, but this loss was counterbalanced by an equally large gain in the rhizomes of the plants cut for hay, but not in those plants which were mown every fortnight. A reduction in the quantity and concentration of carbohydrates in both the roots and rhizomes took place during the summer drought, a far greater loss occurring in the plants which were irrigated than in those which were not. The period most favourable for carbohydrate storage in the roots was between September and November, and, in the rhizomes, from mid-October to November. Thus, although both the roots and rhizomes acted as food stores, they did not show parallel changes in every instance. This lack of correlation was also shown in the results of Weinmann (1947) with *Cynodon dactylon* grown in South Africa. In both the roots and rhizomes, the concentration of available carbohydrates decreased during the spring. In the roots there was a steady increase in the concentration during the summer and autumn, but the concentration in the rhizomes showed only irregular fluctuations during this period, even though they contained the major part of the carbohydrate reserves.

In the rhizomes of *Agropyron repens*, neither Arny (1932), in Minnesota, nor Malahov (1937), in Omsk, were able to find any distinct changes in the carbohydrate content during the summer months, a finding which is in agreement with that of Weinmann concerning *Cynodon dactylon*.

The seasonal changes in the leaf bases have received relatively little attention. Sampson and McCarty (1930) showed that in *Stipa pulchra* the same changes occurred as in the roots (p. 51). Working in the Netherlands, Alberda (1955) studied the water-soluble carbohydrate content of the lowest 5 cm. of shoot growth of *Lolium perenne* plants. He reported that the content was high in spring, fell rapidly during May and then rose gradually until at the end of the year the high spring value was again reached. The carbohydrate content was not determined during the period January to April.

Seasonal Variation of Nitrogenous Substances

Normally, in analysis, only the total or soluble nitrogen content of plant tissue is determined, not the separate nitrogenous compounds. The amount of nitrogen in the underground organs is affected by the rate of its absorption from the soil, its utilisation by the underground organs and its translocation to and from the shoot. In general, the roots lose nitrogen at times of rapid herbage growth and gain it during the autumn. This was the general trend observed by Weinmann (1940a) in three South African grasses (*Trachypogon plumosus*, *Tristachya hispida* and *Digitaria tricholaenoides*). The total-nitrogen content of the roots decreased during the spring and summer, i.e. the period of herbage growth, and increased during the autumn, reaching a maximum during mid-winter. Later

work with *Trachypogon plumosus* (1942) showed that the percentage of both total and water-soluble nitrogen increased in the roots during the autumn while at the same time they decreased in the shoots. He concluded that during this period nitrogen was translocated from the shoots to the roots in the form of water-soluble compounds largely formed by the breakdown of complex organic compounds. The water-soluble compounds accumulated in the roots so that by mid-winter 60% of the total nitrogen was present in this form. These results are in agreement with those of Richardson, Trumble and Shapter (1932) working in Australia with *Phalaris tuberosa*. In work with *Chloris gayana*, Weinmann (1940b) showed that during the autumn, in addition to translocation from the shoot, nitrogen was also accumulated in the roots by simultaneous absorption from the soil.

Other workers have also reported a decrease in the nitrogen content of the underground organs at times of herbage growth and an increase in the content during the autumn. Remy (1923), in Germany, noted that in *Dactylis glomerata* early shoot-growth resulted in a partial depletion of the nitrogen stored in the roots and that replacement took place in the autumn, the maximum nitrogen content in the roots being found in late autumn. Arny (1932) found that in the rhizomes of *Agropyron repens*, the concentration of total nitrogen decreased from May to July and then increased until November. The percentage of amino nitrogen varied very little.

In an investigation extending from April to November, i.e. from the initiation of spring herbage growth until the secondary herbage growth was taking place, McIlvanie (1942) found, in *Agropyron spicatum*, that the percentage of total nitrogen in the roots was near its maximum at the beginning of the investigation. During vegetative development this percentage decreased, and then increased slightly during the rest of the season. No distinct autumn rise was apparent, possibly because the investigation ended too early. The percentage of total nitrogen in the herbage rose rapidly during vegetative growth and then declined during the rest of the season, except for a slight increase at the time of secondary growth. McIlvanie calculated the ratio

$$\frac{\text{percentage reserve carbohydrates}}{\text{percentage total nitrogen}}$$

and found that, initially, this was high in both the root- and shoot-systems. During the time of greatest vegetative growth the ratio was at its lowest, i.e. the carbohydrate stores were utilised to a greater extent than those of nitrogen. At the close of the investigation the ratios were approximately the same as those at the beginning.

Other investigators have not found such well marked trends. Aldous (1930) studying the roots of *Andropogon scoparius*, and Leukel and Coleman (1930) the stolons of *Paspalum notatum*, found no consistent variations in the concentration of nitrogen during the summer months, while Weinmann (1947) was unable to find any significant seasonal trends in the roots and rhizomes of *Cynodon dactylon*.

Seasonal Variation of Minerals

The seasonal variation of the mineral elements shows in many respects the same trends as does nitrogen. According to Richardson, Trumble and Shapter (1932), nitrogen and phosphorus were absorbed rapidly by the roots of *Phalaris tuberosa* during the early stages of growth. Part of this nitrogen and phosphorus was fixed in the plant but some moved from the shoot to the root system as the shoot matured. Calcium was absorbed continuously throughout growth but was soon immobilised within the cells. Potassium remained in a soluble form throughout growth, and, during the final stages, a considerable portion of it was lost from the plant to the soil.

These results for phosphorus are borne out by those of Weinmann (1940a) in South Africa, concerning three native species (*Trachypogon plumosus*, *Tristachya hispida* and *Digitaria tricholaenoides*). The concentration of this element in the roots decreased during the spring and early summer and increased during autumn, reaching a maximum in mid-winter. In *Trachypogon plumosus* it was later found that during autumn the phosphorus was transferred from the leaves to the roots, as a result of which water-soluble phosphorus accumulated in the roots, so that by mid-winter over 80% of the phosphorus was in a water-soluble form (Weinmann, 1942). In *Chloris gayana*, after flowering and during the formation of the seed, considerable quantities of phosphorus and potassium, as well as nitrogen, were lost from the shoots and largely recovered in the roots. These elements also accumulated in the roots as a result of simultaneous absorption.

Further information regarding the autumnal translocation is available from the work of Richardson, Trumble and Shapter (1932) working with *Phalaris tuberosa* in Australia. Considerable losses of nitrogen, potash and phosphoric acid, amounting to 36, 22 and 12%, respectively, of the total intake were found to occur in the herbage during maturation, the herbage not being subjected to any cutting treatments. The losses of nitrogen and phosphorus could be accounted for by gains taking place at the same time in the roots and leaf bases, but potash was lost from both the herbage and the roots, the loss amounting to 27·8% of that in the entire plant shortly before flowering. These workers suggested that this loss took place from the roots by 'diffusion' into the soil.

Working with the grasses of Bechuanaland and the Transvaal, Henrici (1928, 1930) concluded that there was no doubt autumnal re-migration of phosphorus took place from the shoots to the roots. About 40% of the phosphorus remained in the leaves while the haulms were emptied of it to a greater extent. The phosphorus was stored to a greater extent in the root neck than in the roots. A portion of the phosphorus disappeared from the plants during maturation, the only possible channel for its escape being through the roots since the leaves were unbroken at this time. A considerable portion of the phosphorus in the roots and root neck was in a water-soluble form.

The work of Richardson, Trumble and Shapter, Weinmann and Henrici, although carried out under widely differing conditions, shows the same general conclusion that autumnal translocation of minerals from the shoot to the root takes place. Differences in detail may, however, be observed. Thus, Henrici found a loss of phosphorus from the plants while Richardson, Trumble and Shapter did not find a loss of this element, although they found a loss of potassium, an element not studied by Henrici.

Kübler (1954), working with temperate species in Germany, was of the opinion that grasses accumulated nitrogen, phosphorus and potassium in their roots during the late autumn and utilised these stores for herbage growth in the following season. This is in accord with the conception of translocation of minerals from the leaves to the roots in autumn and from roots to leaves during spring and summer. The concentration of calcium in the roots remained constant, as would be expected from the results of Richardson, Trumble and Shapter (1932) (p. 55).

Weinmann (1947) was unable to find any evidence of seasonal variation in the concentration of nitrogen, phosphorus or potassium in the roots or rhizomes of *Cynodon dactylon* grown in South Africa. The reason for this is not clear, but it may be connected with the ability of this grass to withstand adverse conditions in hot climates and with its large food reserve in the rhizomes.

In the young, firm haplocorms of *Phleum pratense*, Trowbridge, Haigh and Moulton (1915) stated that the maximum quantity of potassium was found early in the season while phosphorus tended to increase as the plant and haplocorm matured. They were of the opinion that most of the potassium was absorbed during the early stages of herbage growth while the phosphorus was assimilated throughout the entire growth period. This is not in accordance with the findings of Richardson, Trumble and Shapter.

Defoliation

One effect of defoliation is a reduction in the concentration of reserve carbohydrates in the underground organs, these substances being translocated to the aerial parts of the plant where they are used in the production of new photosynthetic tissue to replace that removed by defoliation. When sufficient new tissue has been formed, the carbohydrates are replaced in the underground organs; that is if environmental conditions are favourable. The effect of defoliation may be apparent for some time afterwards, the quantity and concentration of reserve carbohydrates being less in a defoliated plant than in a control. If defoliation is repeated at frequent intervals, or is carried out at critical times of the year when stores of carbohydrate reserves are low, then the effect is accentuated. The nitrogen and mineral contents are relatively unaffected by defoliation, although some changes in nitrogen metabolism may occur.

Sullivan and Sprague (1943) found that, following the partial defoliation of *Lolium perenne* plants, the concentration of water-soluble carbohydrates (glucose, fructose, sucrose and fructosans) in the roots and stubble decreased rapidly for 11 days. The concentration then remained constant, or increased slightly, for 11 days and then increased rapidly during the following 6 days. Thus, under

the conditions of this investigation (64–68°F. and a 14-hour day) 22 days elapsed before sufficient photosynthetic tissue was produced to enable carbohydrates to be manufactured in excess of those required by current growth. Cellulose, hydrolysable pentosans and lignin failed to show any of these changes, this being taken by Sullivan and Sprague as evidence that the soluble carbohydrates alone act as reserves. Plants placed in darkness after defoliation showed the same changes as those in the light, except that the concentration of soluble carbohydrates continued to decline almost to the point of exhaustion. (Figs. 7 and 8).

Similar results were obtained with *Dactylis glomerata* (Sprague and Sullivan, 1950). In this experiment the plants were clipped three times

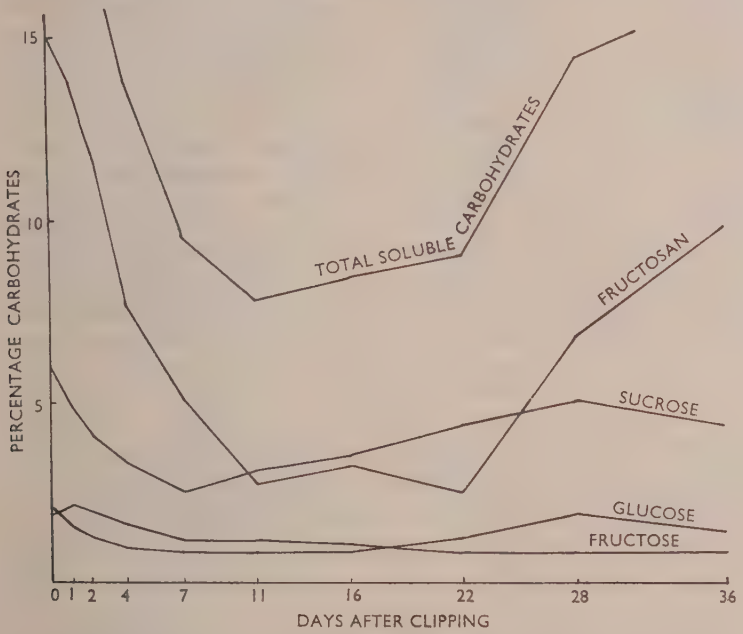


Fig. 7. Water-soluble carbohydrates in the stubble of *Lolium perenne* plants growing in the greenhouse for 36 days after removal of the tops. (*Sullivan and Sprague*, 1943)

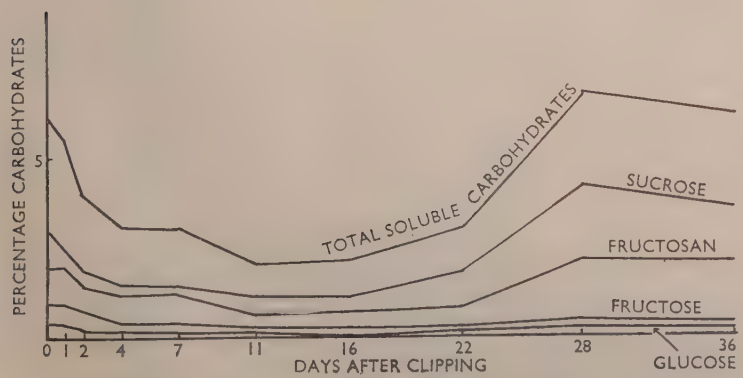


Fig. 8. Water-soluble carbohydrates in the roots of *Lolium perenne* plants growing in the greenhouse for 36 days after removal of the tops. (*Sullivan and Sprague*, 1943)

at 5-week intervals. The stubble and roots went through recurring cyclic changes of chemical composition during the inter-cutting periods. After each defoliation the concentration of fructosan and sucrose in the roots and stubble decreased; the decrease of each fraction was proportional to its concentration, greater decreases occurring, especially in the roots, when concentrations were high. Reducing sugars showed a decrease only when they were present in high concentration, e.g. under conditions of high nitrogen nutrition. After the initial decrease, the concentrations of all soluble carbohydrates were restored to their previous levels before the time of the next defoliation. This experiment was carried out under controlled conditions of 70°F. and a 16-hour day.

In plants of the same species defoliated at the hay stage (plants which had headed but had not yet flowered) the percentage of sucrose in the roots and stubble showed the typical U-shaped curve with the low point occurring 21 days after defoliation (Figs. 11 and 12). The fructosan content was not decreased by this defoliation although it was the dominant water-soluble carbohydrate in the stubble. Sucrose was often the dominant water-soluble carbohydrate in the roots (Sullivan and Sprague, 1953).

As a result of these experiments Sullivan and Sprague suggested that most of the first new tissue formed after defoliation obtained its carbonaceous material primarily, or entirely, from the reserves. After four days the greater part of the carbonaceous matter lost from the reserves was utilised in respiration.

The effect of defoliation practices upon the carbohydrates accumulated at the end of the growing season varies with the intensity of the treatment, i.e. the proportion of photosynthetic tissue allowed to remain on the plant, the number of times treatment is carried out and the times at which it is carried out in relation to seasonal growth. Generally, the higher the proportion of herbage that is removed, the more frequently this operation is carried out and the nearer in time it is performed

TABLE 25

Relative concentration of combined sugar and starch at the end of the third growing season in the roots and stem bases of plants subjected to different modes of partial defoliation during the growing seasons (All clipped to 1in. height above the ground unless otherwise stated)

(*McCarty and Price*, 1942)

	Bromus carinatus	*Agropyron pauciflorum*
Unclipped	100	100
Time of clipping		
Clipped once each season		
Herbage 4in. high	86–94	86–93
Heads high in boot		81–88
Seeds in milk	67–80	67–84
Seed ripe	56–78	60–79
End of season	84–91	89–92
Clipped twice each season		
Herbage 4in. high and 6in. high	73–67	80–86
Herbage 4in. high and seed in milk	66–84	70–79
Herbage 4in. high and seed dissemination begun	77–89	75–85
Heads high and seed dissemination begun	65–76	68–85
Seed in milk and dissemination ended	61–65	69–78
Clipped thrice each season		
Herbage 4in. high, 6in. high and heads showing	87–104	80–90
Herbage 4in. high, 6in. high and 10 days after seed dissemination begun	76–81	85–87
Herbage 6in. high, seed in milk and seed dissemination begun	51–82	66–90
Heads showing, flowers in bloom and seed in dough	73–86	82–87
Ditto, but clipped to a height of 4in.	86–112	86–93
Seed in dough, fully ripe and dissemination ended	78–80	76–87
Clipped frequently during the season		
Every 15 days (8 clippings)	37–49	59–80
Every 15 days (6 clippings to 4in. high).	77–100	71–89

to the period of carbohydrate storage, then the more drastic is the effect upon the concentration and quantity of carbohydrate reserves.

Sampson and McCarty (1930) working with *Stipa pulchra* in Utah, found that the accumulation of carbohydrates in the roots and stem bases took place mainly during the late autumn, and concluded that grazing or removal of the herbage between the time of flower-stalk production and seed maturity prevented maximum accumulation and tended to prolong the vegetative growth of the plant. The concentration of sugars, starch and hydrolysable polysaccharides in the stem bases at the end of the growing season was little affected by harvesting the herbage during the time of slow growth of new herbage in late autumn and winter, but was greatly affected by harvesting during the time of rapid herbage growth in late spring and summer. In later work with *Elymus ambiguus* and *Muehlenbergia gracilis*, McCarty (1935) found that the concentration of sugars and starch in the roots at the end of the growing season (6th September) was reduced by a single clipping of the herbage between July and August, the reduction being roughly proportional to the number of days between the date of clipping and the end of the growth cycle.

Further work on similar lines, but with a more complex system of cutting, was reported by McCarty and Price (1942) (Table 25). They concluded that the concentration of reserve carbohydrates stored in the roots and stem bases at the end of the growing season was related to the amount of herbage present during the normal storage period, which, under the conditions of this investigation, was in August and September. The concentration became less as the interval between the time of clipping and the normal storage period decreased. Removal of the herbage close to the roots (cutting to one inch above the soil) at any time during the storage period reduced the carbohydrate reserves, and, if done at the beginning of this period, not only prevented the normal storage but also stimulated re-growth at the expense of previously stored reserves. If the herbage was clipped early in the season when sufficient time remained for the plant to make new growth and complete the normal growth cycle before the winter, nearly normal carbohydrate storage was attained. All the clipping treatments reduced the concentration of the reserve carbohydrates but did not affect that of the hemicelluloses. A similar result with regard to early and late defoliation was obtained by Klapp (1937a) in Germany.

Working in Kansas with *Andropogon* spp., Aldous (1930) obtained results which would not appear to be in complete agreement with those of McCarty and Klapp. Aldous found that while the concentration of 'reserve' carbohydrates (starch, dextrins and sugars) was reduced at the end of the season in proportion to the length of the interval between clippings, increasing this interval early in the season resulted in a greater concentration of carbohydrates than did increasing it later in the season. The concentration also increased with the increasing height at which the clipping took place.

A decrease in the concentration of reserve carbohydrates in the underground organs at the end of the herbage growth season in proportion to the number of defoliations to which the plant was subjected during the growing season, or, in inverse proportion to the length of the interval between the defoliations, has been reported by several workers, e.g. Sampson and Malmsten (1926), Thaine and Heinrichs (1951), Klapp (1937a), Weinmann (1943, 1944, 1947, 1949) and Thaine (1954). One of Weinmann's experiments

TABLE 26

Chemical composition of the roots of South African highveld grasses (*Trachypogon* veld) as affected by defoliation treatments

(Expressed as percentage of sand-free dry matter)

(*Weinmann*, 1947)

No. of clippings per year	Reducing sugars	Non-reducing sugars	Starch	Starch + sugars	Hemi celluloses	N	P_2O_5	K_2O	Ash
1	0·49	2·73	1·86	5·08	17·0	0·52	0·10	0·47	3·52
2	0·42	2·38	1·77	4·57	16·5	0·56	0·12	0·50	3·62
3	0·43	2·25	1·73	4·41	14·2	0·55	0·12	0·51	3·81
4	0·36	1·50	1·13	2·99	16·4	0·58	0·12	0·39	3·11

TABLE 27

Effect of cutting the herbage during the growing season upon the roots and storage organs at the end of the growing season and their content of reserve substances
(Weights in grams per 100 plants)

(*Klapp*, 1937a)

Number of cuts	Weight of dry mass		Weight of reserve substances		Concentration of reserve substances	
	Actual	Relative	Actual	Relative	Percentage	Relative
			Dactylis glomerata			
4	1007	100	450	100	45	100
3	1294	129	620	138	48	107
2	2293	228	1203	267	53	112
1	2961	294	1579	351	53	112
			Poa pratensis			
4	1040	100	503	100	48·4	100
3	1340	129	694	138	51·7	107
2	1920	185	1003	199	52·2	108
1	2522	243	1260	251	50·0	103

(1943) was conducted on the veld where *Trachypogon plumosus* was the predominant species. The concentration of reducing sugars, non-reducing sugars and starch in the roots decreased with the intensity of defoliation. The percentage of hemicelluloses showed no direct relation to the clipping treatments. (Table 26). The weight of sugars plus starch in the roots decreased to a greater extent than the concentration of these constituents as the total dry weight of the roots also decreased in proportion to the intensity of defoliation. Klapp (1937a) (Table 27), Thaine (1954) and Baker, H. K. (1955) noted similar reductions in other species. In certain of the grasses studied by Weinmann (1944), the concentration of reserve carbohydrates did not always vary with the intensity of defoliation, but the weight of root and carbohydrates did; apparently, most of the old roots lost carbohydrates and died, but a few roots, possibly young ones, with a high concentration of carbohydrates survived (Table 28).

Grazing was found by Weinmann (1948c) to have the same effect as clipping in that heavy grazing reduced both the weight of roots and the concentration of reserve carbohydrates in them to a greater extent than moderate grazing. Grazing over a number of years was reported by Hanson and Stoddart (1940) to decrease the concentration of sugars and starch in the roots and leaf bases of *Agropyron inerme*, but not to affect the concentration of hemicellulose.

Defoliation has almost the same effect upon the leaf bases as it has upon the roots. This was the finding of Sampson and McCarty (1930) working with *Stipa pulchra*, Sullivan and Sprague, (1943, 1953) and Sprague and Sullivan (1950) working with *Lolium perenne* and *Dactylis glomerata* (Figs. 7, 8, 9, 10, 11 and 12). Similar results to those of Sullivan and Sprague with the water-soluble carbohydrate content of *Lolium perenne* plants were obtained by Alberda (1955), who also noted that when the time of defoliation coincided with the seasonal spring fall in carbohydrate content that the decrease in the percentage of this constituent could be very great indeed.

Ahlgren, H. L. (1938) investigated the effect of clipping the herbage of *Poa pratensis* plants upon the concentration of total carbohydrates in their rhizomes. Clipping the herbage to 1·5 in. every time it reached a height of 4–5 in. resulted in a gradual increase in the concentration of carbohydrates throughout the period of the investigation (June to November). Deferring the start of cutting until the plants were in the 'early heading' or 'fully headed to mature' stage resulted in a higher concentration of carbohydrates in the rhizomes, but there was no continuous increase in the concentration throughout the season as there was in the rhizomes of plants which were defoliated from the beginning of the experiment. In the plants which were not subjected to defoliation until late in the season a decrease in concentration of carbohydrates in the rhizomes occurred after the first cut; this was most marked in the plants not cut until they were 'fully headed to mature'. The older the plant at the time of its first defoliation then the more erect was its growth habit, i.e. the greater the proportion of leaves above

the level of the cut. Ahlgren attributed the decrease in carbohydrate concentration in the older plants after the first defoliation to the removal of a greater proportion of the herbage making greater demands upon the carbohydrate stores.

The effect of different systems of herbage management in the previous growing season upon the chemical composition in November of the haplocorms of new shoots of *Phleum pratense* was studied by Smelov (1937). Both the water-soluble carbohydrates and hemicellulose concentrations were reduced by mowing the herbage four times instead of twice. Late cutting of the aftermath caused a greater reduction in the concentration of water-soluble carbohydrates than did early mowing, presumably due to reserves being used to produce herbage growth which was unable to replace them by photosynthetic activity before the onset of winter. Knoblauch, Ahlgren and Gausman (1955) found that the defoliation of swards of *Phleum pratense* at the 'early heading' stage reduced the weight of haplocorms in the autumn compared with plants defoliated at 'beginning to bloom' and 'late bloom' stages. The percentage of carbohydrates and nitrogen in the corms was affected to the same extent by these defoliation treatments so that the quantity of reserves varied with the weight of the corms.

Several investigators have reported an increase in the concentration of nitrogen, especially soluble nitrogen, in the underground organs following defoliation, and have attributed this to increased absorption from the soil, hydrolysis of proteins, and, when the results were reported as percentages, to relative increases due to loss of carbohydrates. Other investigators, however, have not found any such increase.

In the stubble of *Lolium perenne* plants, Sullivan and Sprague (1943) found that the percentage of both total and insoluble nitrogen decreased the first day after partial defoliation but then increased rapidly for 6 days. The proportion of nitrogen in a soluble form increased from 17% at the time of cutting to 22% seven days later. In plants which were kept in darkness after defoliation the proportion of soluble nitrogen increased very rapidly for 28 days and amounted to 49% of the total at the end of this period. One-quarter of this soluble nitrogen existed as nitrates, which were not detected prior to defoliation but which accumulated rapidly in the plants kept in the dark, and later decreased as the plants were

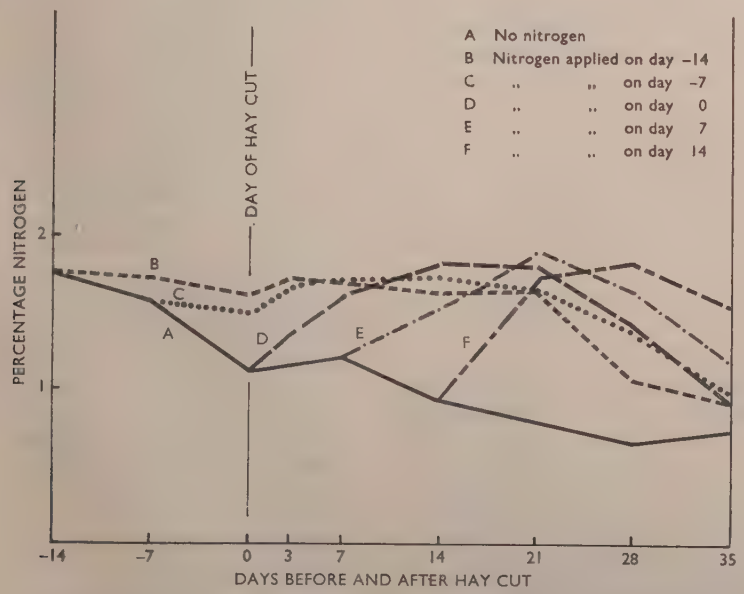


Fig. 9. Changes in the total nitrogen in the stubble of *Dactylis glomerata* plants, in percentage of the dry weight. (*Sullivan and Sprague*, 1953)

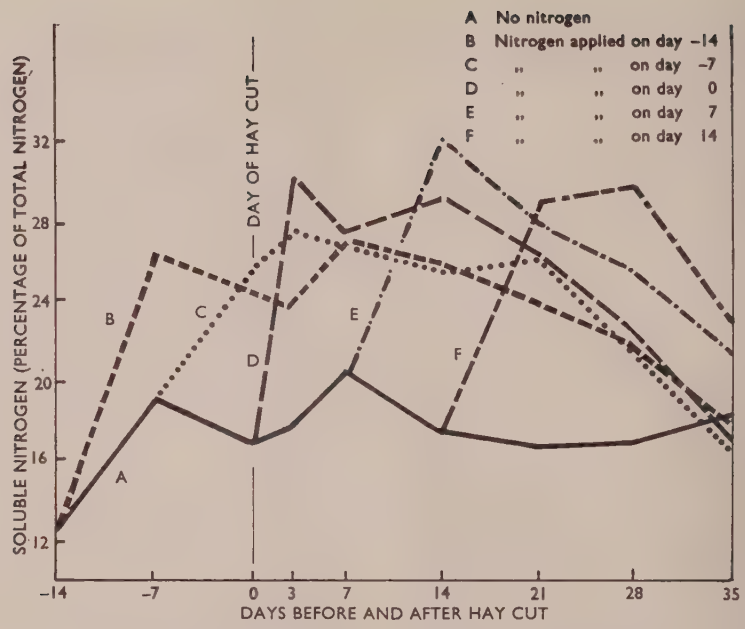


Fig. 10. Changes in soluble nitrogen in the stubble of *Dactylis glomerata* plants, in percentage of total nitrogen. (*Sullivan and Sprague*, 1953)

dying. The total nitrogen in the roots showed less fluctuation than that of the stubble. The concentration declined for seven days after defoliation, not for one day only as it did in the stubble. The proportion of the nitrogen in a soluble form increased, especially in the plants kept in darkness.

In later work, Sullivan and Sprague (1953) found that similar changes took place in the roots and stubble of *Dactylis glomerata*, although they could be greatly modified by the application of a nitrogenous fertilizer (Figs. 9 and 10). They suggested that the increased soluble nitrogen could originate from either protein hydrolysis or from increased absorption by the roots.

The cutting of the herbage of plants of *Agropyron spicatum* during the period of spring vegetative growth (cut every 2 weeks for 8 weeks) was found by McIlvanie (1942) to increase the percentage of nitrogen in the roots and to decrease it in the herbage. This latter result would seem to be rather unusual. Clipping also reduced the concentration of reserve carbohydrates and the ratio $\frac{\text{percentage reserve carbohydrates}}{\text{percentage total nitrogen}}$ in both the roots and shoots. This is in accordance with the results of Nikitina (1940) who found that defoliation treatments reduced the carbohydrate reserves to a greater extent than those of protein in the roots of several species. Richardson, Trumble and Shapter (1932) found that in the roots and leaf bases of *Phalaris tuberosa* the quantity of nitrogen decreased with increasing intensity of defoliation, as did the dry weight of these parts. The percentage of nitrogen, however, increased. In the stolons and shoots of *Paspalum notatum*, the concentration and quantity of nitrogen was reported by Leukel and Coleman (1930) to increase with the severity of defoliation, but the nitrogen of the roots was almost unaffected.

Other workers have reported that the concentration of nitrogen in the underground parts could not be related to defoliation treatments, e.g. Burkey and Weaver (1939) working with *Andropogon* spp., and Johnson and Dexter (1939) with the rhizomes of *Agropyron repens*. Weinmann (1943 and 1948c) found that the nitrogen concentration in the roots of South African high-veld grasses was unaltered by clipping treatments but was increased by grazing. In both instances the

quantity of nitrogen decreased with the decrease in the weight of dry matter.

The quantity of minerals in the underground parts apparently decreases with the severity of defoliation, as does the dry weight of these parts. This was found by Leukel and Coleman (1930), with phosphorus and potassium in the roots and stolons of *Paspalum notatum*. The quantity of phosphorus in the roots and 'butts' of *Phalaris tuberosa* was noted by Richardson, Trumble and Shapter (1932) to decrease in the same manner. The percentage in the butts increased with defoliation intensity but no increase in the percentage in the roots took place, except under the most severe treatment (clipping 5 times per year). Weinmann (1943, 1948c), however, reported that severe defoliation (clipping 8 times per year) had an adverse effect upon the concentration of phosphorus and potassium in the roots of South African highveld grasses. Milder defoliation treatments and grazing had no effect. The quantity of these elements decreased with the dry weight in proportion to the severity of the defoliation treatment. The percentages of nitrogen, acid-soluble ash and phosphorus in the roots of grasses in Marandellas sandveld (chiefly *Eriosema englerianum*) were found by Weinmann (1949) to be unaffected by the frequency of defoliation, but the potassium content of the stem bases was found to fall distinctly with greater frequency of cutting while the calcium content increased; in the roots the calcium content was also slightly higher in the more frequently cut plants. Burkey and Weaver (1939) found that the concentration of ash in the roots of *Andropogon* spp. was unaffected by defoliation treatments, although the concentration of hydrolysable carbohydrates was reduced in the normal manner.

The relationship between the reserves in the roots and stubble of plants of *Dactylis glomerata* and the shoot growth following partial defoliation has been the subject of some preliminary investigations by Sullivan and Sprague (1953). Greater aftermath yields 25 days after cutting were obtained from the larger plants, these plants not being particularly different from smaller ones on the basis of the percentage of carbohydrate reserves but somewhat lower in percentage of nitrogen, a common result with pot-grown plants. This limited evidence did not show that aftermath production was particularly dependent upon the level of carbohydrate reserves. Rhizomes of *Cynodon dactylon*, allowed to sprout in moist sand in the laboratory, have been shown to utilise stored carbohydrates for growth, and determinations of shoot and root growth have indicated that most of the carbohydrate was used in respiration (Weinmann, 1947).

As measured by the resulting depletion of carbohydrate reserves, *Poa pratensis* has been reported to be more resistant to defoliation than either *Bromus inermis* (Smelov, 1937) or *Dactylis glomerata* (Klapp, 1937a) (Table 27). This has been attributed to its prostrate growth habit which resulted in the removal of a smaller proportion of the photosynthetic tissue than was the case with the other species. A similar explanation was put forward by Weinmann (1947) to explain the resistance of *Cynodon dactylon*, a very prostrate species, to clipping treatments. In plants of this species no relationship was found, after two seasons, between the percentage of available carbohydrates in the roots and rhizomes and the severity of defoliation, although the severity varied between cutting high once a month to cutting low thrice a week. If, however, the plants were completely defoliated once a week, using scissors, a marked decrease in the carbohydrate reserves took place. It is of interest that Hughes (1937) reported that the nitrogen and ash content of the roots and rhizomes of *Poa pratensis* were unaffected by clipping treatments to which the plants were subjected (cf. Ahlgren, H. L., 1938) (pp. 60–1).

Mineral Nutrition

The effect of an application of fertilizer on the underground organs of a grass plant would be expected to vary with the environmental conditions, especially the initial composition of the growth medium, and the species studied. Several investigators have reported that the phosphorus and nitrogen contents of the underground organs have been increased by the application of an appropriate fertilizer. The concentration of both these elements in the roots of native species on the South African Veld was found by Weinmann (1940a and b, 1942, 1943, 1947, 1948c) to be increased as a result of the application of an NPK fertilizer. Only the phosphorus content was increased by a PK fertilizer; the potassium content in general was not affected by either fertilizer. Hughes (1937) stated that an NPK fertilizer increased the concentration of nitrogen in the roots

TABLE 28

Dry weight of roots (grams per sq. decimetre) (1) and the weight (milligrams per sq. decimetre) (2) and percentage (3) of sugars plus starch in the roots of four species as influenced by defoliation treatments

(*Weinmann*, 1944)

Species		Number of cuts per season: 1			2			4			9			16		
		Criteria: 1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Trachypogon plumosus	O	4·78	399	8·31	5·37	357	6·65	2·80	128	4·58	0·85	15	1·72	0·66	14	2·08
	NPK	6·73	635	9·44	5·62	493	8·79	3·00	220	7·33	0·63	28	4·41	0·42	6	1·40
Tristachya hispida	O	4·92	590	12·02	6·50	675	10·38	3·85	310	8·05	2·54	38	1·50	2·26	20	0·88
	NPK	7·62	817	10·73	9·60	1010	10·54	7·33	632	8·62	1·85	26	1·40	1·21	15	1·20
Eragrostis chalcantha	O	3·64	196	5·37	3·66	155	4·23	2·42	90	3·71	0·28	11	4·06	0·02	*	*
	NPK	7·38	462	6·25	9·90	443	4·47	2·45	80	3·26	0·27	12	4·62	0·04	*	*
Brachiaria serrata	O	10·20	780	7·65	15·33	1040	6·78	1·68	55	3·27	0·63	20	3·17	2·16	25	1·15
	NPK	12·32	963	7·83	11·23	477	4·25	1·53	26	2·33	1·09	32	2·98	1·01	21	2·09

* Not determined for lack of material.

and rhizomes of *Poa pratensis*, and Sprague, H. B. (1934) found that the phosphorus content in the roots of *Agrostis tenuis* and *Poa pratensis* increased as a result of an increased phosphorus concentration in the growth media. According to Nad'jarnyi (1939), an NPK fertilizer increased the phosphorus content of the roots and stubble of *Agropyron* sp. and *Trifolium repens*.

Bronzova (1940) stated that the application of an NPK fertilizer, under a moderate intensity of defoliation, increased both the dry weight of roots of *Bromus inermis* and *Phleum pratense* and the concentration of carbohydrates. In certain of Weinmann's experiments (1943, 1944) there was an interaction between the application of an NPK fertilizer and the intensity of defoliation. When the plants were defoliated infrequently, the weight of starch plus sugar in the roots was increased by the fertilizer, but when defoliated frequently the fertilizer reduced this weight. This was due to the action of the fertilizer upon the dry weight of the root rather than on the concentration of starch and sugar (Tables 28 and 29). In general, in the experiment reported in the 1943 paper the two NPK treatments increased the concentration of sugar but reduced that of the starch. A PK fertilizer reduced the weight of starch and sugars under all except the most severe defoliation treatments. The interaction between the fertilizer and defoliation treatments therefore was evidently due to the nitrogen content of the fertilizer. The concentration of acid-hydrolysable polysaccharides (hemicelluloses) in the roots of Weinmann's plants was unaffected by these defoliation and fertilizer treatments. Knoblauch, Ahlgren and Gausman (1955) working in New Jersey stated that the application of an NPK or a N fertilizer to swards of *Phleum pratense* during the growing season resulted in an increased weight of corms in the following autumn and an increase in the carbohydrate and nitrogen content of the corms.

TABLE 29

Dry weight of roots (1), the weight (2) and percentage (3) of sugars plus starch in the roots of South African highveld grasses as affected by fertilizer and defoliation treatments
(Weights in grams per two square-metre quadrat)

(*Weinmann*, 1943)

	Fertilizer treatment											
	O			PK			PK + $(NH_4)_2SO_4$			PK + $NaNO_3$		
	Criteria											
	1	2	3	1	2	3	1	2	3	1	2	3
No. of clippings												
1	583	29·6	5·08	418	20·1	4·80	556	30·1	5·41	592	27·8	4·69
2	483	22·1	4·57	385	16·9	4·39	433	22·4	5·18	567	29·3	5·17
4	286	12·6	4·41	256	8·5	3·31	443	19·0	4·24	366	16·9	4·61
8	204	6·1	2·79	217	5·6	2·60	177	6·2	3·49	204	7·2	3·52

Nitrogen Nutrition

According to Benedict and Brown (1944) one of the principal effects of lowering the concentration of nitrogen in the growth medium was to increase the concentration and quantity of starch and sucrose in both the roots and shoots of plants of *Agropyron smithii*, and of sucrose in plants of *Bouteloua gracilis*; the starch content of the latter remained unchanged. The general effect of making nitrogen available to plants which had been without it for sometime was to reduce the concentration of carbohydrates built up when nitrogen was lacking.

Similar results were obtained by Sprague and Sullivan (1950) with plants of *Dactylis glomerata* which were partially defoliated every 35 days. Under conditions of high nitrogen nutrition, the percentages of fructosan and sucrose in the roots and stubble were less, but the percentage of reducing sugars was higher, than under low nitrogen nutrition. The addition of nitrogen to plants previously under low nitrogen nutrition resulted in decreases in the fructosan and sucrose contents. The reducing sugars were not affected immediately, but striking increases occurred in the concentration a few weeks later, after which they apparently acted as reserve substances.

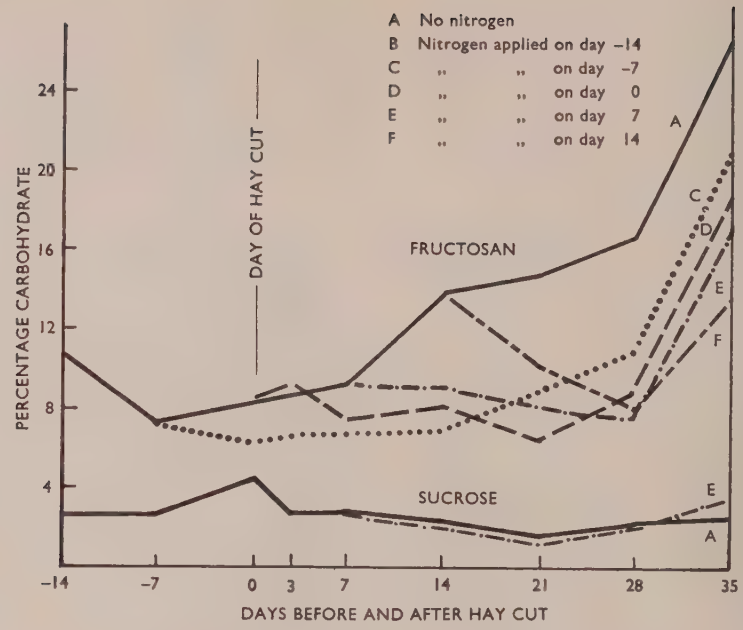


Fig. 11. Changes of fructosan and sucrose in the stubble of *Dactylis glomerata* plants, in percentage of the dry weight. (*Sullivan and Sprague*, 1953)

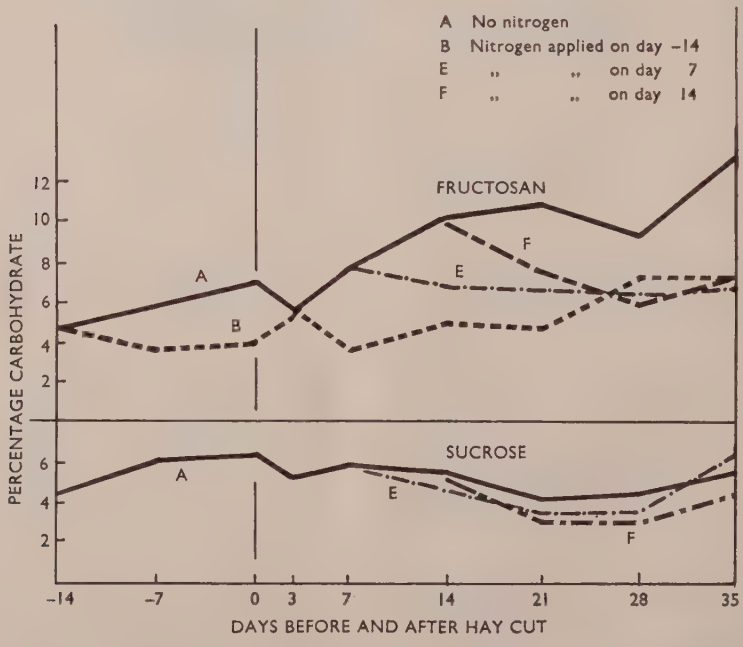


Fig. 12. Changes of fructosan and sucrose in the roots of *Dactylis glomerata* plants, in percentage of the dry weight. (*Sullivan and Sprague*, 1953)

This work was taken further (Sullivan and Sprague, 1953) by studying the time of application of nitrogenous fertilizer in relation to partial defoliation. The addition of nitrogenous fertilizer to the growth medium resulted in an immediate decline in the percentage of fructosan and sucrose in both the roots and the stubble, irrespective of the time of application. The difference between the fertilized and unfertilized plants tended to decrease as time advanced (Figs. 11 and 12).

The results of Watkins (1940) with *Bromus inermis* in the field (the other experiments were carried out in 'artificial' environments) are not so conclusive. The proportion of sugars and easily hydrolysed carbohydrates in the stubble, roots and rhizomes showed no consistent effect due to the application of a nitrogenous fertilizer. The dry weight of rhizomes was decreased and that of the roots increased early in the season, but both were decreased later by the nitrogenous fertilizer.

Nearly all investigators have reported that high nitrogen nutrition resulted in a high concentration of nitrogen in the underground organs. Watkins (1940) reported that this occurred in the roots and rhizomes of *Bromus inermis*, Johnson and Dexter (1939) in the rhizomes of *Agropyron repens* and Sprague, H. B. (1934) in the roots of *Poa pratensis* and *Agrostis tenuis*. Sullivan and Sprague (1953) found that, in the roots and stubble of *Dactylis glomerata*, nitrogenous fertilizer increased the concentration of soluble nitrogen to a greater extent than the total nitrogen mainly because of increased absorption of nitrogen from the soil.

Temperature

Plants of *Poa pratensis*, *Poa compressa*, *Dactylis glomerata* and *Cynodon dactylon* were grown by Brown, E. M. (1939) at soil temperatures of 40 to 100° F. for 8 weeks. (For further details of the experiment see p. 81 *et seq.*) At the end of this period, the concentration of 'nitrogen-free extract' in all the parts (roots, shoots and rhizomes) of the plants with a low optimum growth temperature (i.e. *Poa* spp., *Dactylis glomerata*) decreased with increasing temperature, while the concentration in *Cynodon dactylon*, a species with a high optimum growth temperature, increased. The percentage of 'crude protein' declined slightly in the three 'low temperature' species from 40 to 60° F. and then increased slightly as the temperature rose above the optimum for growth. In *Cynodon dactylon* the concentration of 'crude protein' was much greater at 50° F. than at 60°F., the percentage remaining more or less constant with any further increases in temperature. In all four grasses the concentration of 'crude fibre' increased as the temperature rose from 40 to 60° F. and then changed little with further increases in temperature. So far as chemical composition was concerned, a high day-temperature appeared to be counterbalanced by a low night-temperature. Brown was of the opinion that these results supported the view that, at temperatures above the optimum for growth, the carbohydrate balance of the plant was disturbed by the failure of carbon assimilation to keep pace with carbon loss by respiration. He also concluded that there was strong evidence that nitrogen tended to accumulate in the plant at temperatures too low for normal development.

Sullivan and Sprague (1949) studied the recovery of plants of *Lolium perenne* from the clipping of the herbage when grown under four temperatures (50–60, 60–70, 70–80 and 80–90°F.). The temperature treatments were begun at the time of defoliation. New shoot growth was most rapid at 60–70° and least at 80–90° F. In all four temperature treatments, the dry weight of both the roots and the stubble decreased throughout the 40 days after clipping during which they were studied, the losses being most rapid and extensive at the higher temperatures. The roots and stubble also underwent rapid losses of sucrose and fructosan during the early part of the experiment but these losses, were, under low temperature conditions, partially replaced later. Under high temperatures, especially in the roots, the losses continued almost to the point of exhaustion and in some cases until the death of the roots. Protein metabolism was characterised by an increase in the proportion of soluble nitrogen immediately after the leaves were clipped, and, at the highest temperatures, this proportion continued to increase for a long time in the shoots and stubble. High temperatures, leading to the rapid dissipation of reserve carbohydrates, slowed down the production of new leaf growth, and, in general, inhibited the recovery from defoliation.

Drought

During a drought, (i.e. lack of water, frequently accompanied by high temperature) a

plant usually makes little or no growth and the carbohydrate reserves change very little. If growth is stimulated by partial defoliation or by the addition of water to the growth medium then carbohydrate reserves are lost.

This was shown by Julander (1945) working in the U.S.A. Any interference with plants of *Cynodon dactylon* or *Buchloë dactyloides* by clipping the herbage or adding water to the soil during a period of drought caused a reduction in the percentage of reducing sugars and glucosans in the roots at the end of the experimental period. Watering had a greater effect than clipping. This effect of watering was also noted by Brown, E. M. (1943) in Missouri. During a summer drought a decrease occurred in the starch and sugar content of the rhizomes of all plants of *Poa pratensis*, but the decrease was far greater in those plants which were irrigated than in those which were not.

Investigations with *Agropyron* and *Andropogon* spp. by Julander showed that plants usually accumulated carbohydrate reserves (sugars, levulosans and glucosans) during drought periods, but that this was prevented by over-grazing or severe clipping. A large accumulation of colloidal carbohydrates, especially levulosans, was associated with drought resistance. In all Julander's experiments a decrease in carbohydrate reserves was associated with a decrease in heat resistance.

Burkey and Weaver (1939) found that the concentration of hydrolysable carbohydrates in the roots of *Andropogon* spp. was reduced by a summer drought, which is in agreement with Brown's results, but not with those of Julander. The reason for this discrepancy may lie in the relative 'degree' of drought to which the plants were subjected or in the species' adaptation to drought.

Light Received by the Shoot

The findings of Sullivan and Sprague (1943) concerning the effect of keeping plants of *Lolium perenne* in darkness after partial defoliation have already been mentioned (p. 57). Plants kept in darkness underwent similar chemical changes to those kept in the light, except that the carbohydrate reserves were depleted almost to the point of exhaustion and the hydrolysis of proteins took place to a greater extent. The plants placed in darkness behaved in some respects like those subjected to high temperatures: both environmental conditions led to a rapid dissipation of carbohydrate reserve and to the digestion of protein. The plants in darkness, however, accumulated a high concentration of nitrates in the roots which disappeared before the death of the plants. No nitrates were found in the plants kept at high temperatures, but this may have been due to differences in the growth media, the plants kept in darkness having been grown in nutrient solution in gravel, whilst those kept at high temperatures were grown in soil (Sullivan and Sprague, 1949).

The shading of plants of *Bromus inermis*, grown in Ohio, was reported by Watkins (1940) to greatly reduce the yield of roots, rhizomes and stubble and to reduce slightly the yield of hay. It also reduced the concentration of reserve carbohydrates (sugars and easily hydrolysed carbohydrates) in all parts. The quantity of reserve carbohydrates in the underground organs was thus greatly reduced. The concentration of total nitrogen was increased slightly by the shading.

Watkins also studied the effects of short (8·5 hour), normal (15-hour) and long (18-hour) daylengths. The concentration of reserve carbohydrates was highest in the hay and stubble grown under long days, while the carbohydrate concentration in the roots and rhizomes increased slightly with daylength. The weight of all plant parts increased with the length of day, but the hay and rhizomes increased to a greater extent than the roots or stubble. With the increase in the length of day the percentage of total nitrogen decreased in the hay and stubble, remained constant in the roots and increased in the rhizomes.

CHAPTER 13

ROOT EXUDATES

The subject of root exudates in general has been discussed by Loehwing (1937), Russell, E. J. (1950) and Bonner (1950), but not with particular reference to grasses.

The elimination of inorganic salts, especially phosphatic compounds, from the roots of legumes and certain other crops when grown in soil cultures appears to occur normally after flower formation (Loehwing, 1937). By ascertaining the quantity of minerals in plants at intervals throughout the growth cycle, Richardson, Trumble and Shapter (1932) showed that potassium, but not phosphorus, was lost from *Phalaris tuberosa* at this time, while Henrici (1928, 1930) found that phosphorus was lost from grasses in Bechuanaland and the Transvaal (p. 56).

The evidence concerning the excretion of organic compounds is of a more complex nature. Germinating seeds and young seedlings grown in water culture have been reported by several investigators to produce exudates. Gentner (1929) discovered that the roots of seedlings of *Lolium multiflorum* grown on white filter paper would bring about a condition in the paper so that when it was examined under ultra-violet light it was rendered fluorescent. The seedlings of *Lolium perenne* did not produce this effect. This is the basis of the Gentner Test for differentiating between the species of *Lolium*. In general this character appears to accompany shortness of life in a species and is inherited along Mendelian lines (Justice, 1945–6). Other species of Gramineae show this phenomenon to a lesser extent (Foy, 1931). Foy (1931) has suggested that the exudates consist of one or more enzymes which attack the constituents of the paper.

More evidence comes from Osvald's (1949) experiment. He germinated and grew seeds of several grasses on moist filter papers. After three weeks the grass seedlings were removed and rape seeds were germinated on the papers. The grass-root exudates absorbed by the papers during the three-weeks' growth of grass had only a slight adverse effect on the percentage germination of the rape, but they had an obvious and deleterious effect on the production of seedling roots. These effects could be related to the quantity of roots produced by the grass seedlings, the species producing most roots having most effect. This experiment may be criticised on the grounds that not all the roots of the grass seedling were removed from the filter papers and so some of the effects may have been due, in part at least, to the presence of the decaying grass roots. Further evidence of this nature is available from the work of Triffit (1934) who found that the number of viable larvae hatched from cysts of *Heterodera schachtii* was increased by their treatment with water in which grass seeds had germinated. Brown and his co-workers (Brown, Johnson, Robinson and Todd, 1949; Brown, Robinson and Johnson, 1949) found that a concentrate of water in which intact roots of seedlings of *Sorghum vulgare* had been grown would stimulate the germination of seeds of *Striga hermonthica* and the growth of the excised roots of *Pisum sativum* and *Zea mays*. The concentrate contained carbohydrates particularly pentoses. The sugar D-xyloketose had similar actions on the seeds and roots as the concentrate, and it was deduced that the concentrate contained a substance similar to D-xyloketose.

The only exudates other than inorganic salts, reported from mature roots, are those which have an effect on living matter. Osvald (1947) found that an aqueous or ammonia-solution extract of *Agropyron repens* roots contained a substance which affected the germination of rape and oat (*Avena* spp.) seeds. At very low concentrations the germination of these species was promoted, at somewhat higher concentrations it was retarded, while a still higher concentration inhibited germination. Having observed that oats and rape in the field germinated and developed poorly on patches of ground occupied by *Agropyron repens*, Osvald concluded that this species excreted through its roots a substance similar to that found in the extract. This worker (1949) carried out a similar experiment with ammonia-solution extracts of soil from a *Festuca rubra* meadow and soil from arable land. The *Festuca rubra* soil extract had a detrimental effect on the germination of rape seeds while the arable-soil extract had no effect. The harmful effect of the *F. rubra* soil extract was destroyed by heating at 176–194°F.

Osvald also found that the extract from the roots of *Agropyron repens* at moderate to high concentrations favoured the growth of mould fungi, but that very high concentrations retarded growth. Similarly, Stiven (1952) found that a water extract of the roots of *Trachypogon plumosus* inhibited the growth of bacteria.

Triffitt (1934) followed her work on the germination of grasses with pot and field experiments. She found that the number of viable larvae hatched from cysts of *Heterodera schachtii* was increased in pots growing grasses as compared with pots growing other plant species, excluding the normal host species. *Poa pratensis* and *Poa trivialis* were the most effective species in producing hatching. It was also found that more larvae of *Heterodera schachtii* hatched in a field sown to grass than in an arable field.

The results of Osvald are not supported by the work of Guyot, Becker, Massenot and Montigut (1951) who stated that water extracts of the roots, and the soil in contact with the roots, of *Brachypodium pinnatum* had no effect on the germinating seeds of several species, although similar extracts of plants of fifteen non-graminaceous species were toxic in varying degrees.

Bedford and Pickering (1914) in England, after noticing that a check in the growth of the trees occurred when an orchard was grassed down, conducted a series of experiments in which plants were watered with leachings from soil growing grass and from soil without a crop. The former plants made less growth than the latter. As a result of these experiments they formulated a theory that 'every growing crop results in the formation of a substance which is toxic to the growth of other plants and more so to itself'. This theory was doubted by Russell, E. J. (1935) who stated that the results observed by Bedford and Pickering in fruit trees could be induced by nitrogen starvation. The suggestion of nitrogen starvation derives support from Howard's (1925) experiments which showed that the deleterious effect of grass on fruit trees could be overcome by applying nitrogenous fertilizers to the trees. A more recent view is that check in growth to the tree is due to competition between the trees and grass for nitrogen and water (Greenham, 1952), (p. 119).

In view of the above results from fruit trees it is of interest to recall that many claims have been made to the effect that the growing crop interferes with the production of nitrates in the soil (Russell, E. J., 1950). Theron (1951) found that nitrates were not present in the leachings from lysimeters under a grass sward of *Hyparrhenia* sp., from the second season onwards. Earlier workers had noticed similar effects and had postulated that plant roots excreted large amounts of carbonaceous matter causing the nitrates to be assimilated by micro-organisms. Theron rejected this theory on the grounds that more carbonaceous matter would be needed than the plants could produce. Instead, he concluded that the plants exert their influence, possibly through root excretions, by paralysing the autotrophic dehydrogenase system of the nitrifying micro-organisms without interfering with the process of ammonification. Another worker (Stiven, 1952) has also suggested that the roots of a grass may excrete an antibiotic substance which inhibits the nitrifying bacteria. He based his theory on the facts that a soil growing *Trachypogon plumosus* did not contain nitrates and that a water extract of the roots of this species inhibited the growth of bacteria. Walker, Orchiston and Adams (1954) have, however, pointed out that it is quite possible for the decomposition of old grass roots to result in the immobilisation of much, if not all, of the mineralised nitrogen produced in the soil, thus accounting for the apparent cessation of nitrification in soils growing grasses. The antibiotic theory of Stiven is, however, supported by the results of Roux (1953). Nutrient solution which had passed through sand in which plants of *Trachypogon plumosus* were growing was found to reduce the germination of the seeds of *Tagetes minuta*, compared with a solution which had been passed through sand not growing any plants. In addition, the seedlings which were produced from the seeds treated with the solution from the *Trachypogon* cultures showed a distinct browning and curling of the roots, features which were absent in the controls.

Certain Russian workers have put forward the view that grass roots excrete substances which are used by bacteria to form soil aggregates (Suchalkina and Kotlyarov, 1949; Gel'tser, 1944) (p. 127).

All the experiments reporting root exudates are open to criticism. The effect of the various extracts may be attributed to the action of substances found in the cell but not excreted (Osvald, 1949). This, however, would not explain the observations in water cultures. In non-gramineous

species it has been shown that many of the substances reported as secretions were actually disintegrated and highly dispersed tissues which had been abraded from the roots during the natural process of growth (Loehwing, 1937). The evidence in every experiment quoted previously, except that of Gentner, of the existence of a substance which may be an exudate depends upon the substances acting on living material. No compound has been collected from the roots and identified. The evidence, except in the case of inorganic salts, is circumstantial and further work is required before the subject can be better understood.

PART II

FACTORS INFLUENCING GROWTH

The growth of a grass plant is a multi-conditioned response to its environment. Provided a plant is capable of growth then the rate of growth at a particular time will depend upon the relative concentrations in which the factors essential for growth are present, and will be largely controlled by the concentration of that factor which is present in the relative minimum, i.e. the 'limiting factor'. This assumes the absence of inhibitory substances or a harmful excess of one or more growth factors. Variations in the concentration of one or more of the essential growth factors may not affect growth in all parts of a plant, or plants of different genetic constitution, to the same extent or in the same manner. Injury to a plant, either by defoliation or by root pruning, has a similar effect to an increase in the quantity of a growth factor in that it stimulates the growth of the part of the plant concerned.

Most of the studies considered in this section were carried out on young plants so that the presence of old decaying roots would not mask any growth by younger roots. Care needs to be taken when considering the results of any experiment involving plants over approximately six months old, as both decay and growth may be taking place.

In this section the relationship between root and shoot has largely been expressed as the percentage of the plant's weight in the roots, i.e.,

$$\frac{\text{weight of roots}}{\text{weight of roots plus shoots}} \times 100$$

Troughton (1955b) has pointed out the danger of using such ratios of plant proportions for comparative purposes on account of the difficulty of separating the differences due to variations in the size of the plants that are being compared and the differences due to the experimental treatments. This, however, is the only method which can be used with most of the published data. In most of the experiments plants were measured only once, at the end of the experimental period, so that the allometric formula or other methods of comparison, such as growth curves, cannot be used (see p. 29).

CHAPTER 14

SOIL WATER

The whole subject of the relationship between plant growth and soil water has been reviewed by Kramer (1949), Russell, E. J. (1950) and Shaw (1952).

A deficiency of water results in poor growth being made by both the roots and shoots of grass plants. An increase in the amount of water in the soil results, in most environments, in an increase in shoot- relative to root-growth i.e. the percentage of the plant's weight in the roots decreases. The root systems of grasses are able to adapt themselves to the available water supplies by varying the distribution of the roots in the soil. Thus, in situations where precipitation is the chief source of supply, a lack of it tends to cause the roots to concentrate in the upper layers of the soil. A raising of the soil's water-table also causes the roots to concentrate in the upper layers of the soil, possibly through lack of aeration; and a low water-table, provided it is not too deep, encourages the plants to be deep-rooting.

An experiment in which the effect of a wide range of soil-water contents was investigated is that reported by Kauter (1933) who grew plants

from the time of germination in soil whose water content was kept constant at 40, 55, 70, 85 or 100% of its water capacity (Figs. 13 and 14). At the end of one growing season, *Alopecurus pratensis* and *Agrostis alba* had made most root growth at 100% water capacity; *Lolium italicum*, *Festuca pratensis*, *Phleum pratense* and *Trisetum flavescens* at 85%, *Dactylis glomerata* at 70% and *Arrhenatherum elatius* at 55%. All species except *Dactylis glomerata* made most herbage growth at 85%. Thus the percentage of the plant's weight in the roots decreased when the soil's water content was increased from 40 to 85%, but increased when the water content was increased from 85 to 100%. The species studied varied greatly in their relative reaction to moisture contents above and below the optimum for root growth.

An experiment of an entirely different nature but again including a wide range of treatments was that reported by Schuurman and Makkink (1955). An established mixed sward in the Netherlands was subjected to several overhead irrigation treatments from May to October. The plots were cut once per month and received 50 kg. of N per ha. (approximately 0·5 cwt. per acre) after each cutting. At the end of this period the total weight of roots under each plot was determined. The highest weight of roots was found in the 'dry' plots (these received a total of 298 mm. of rain plus water from the irrigation treatment) and the 'very wet' plots (these plots received a total of 966 mm. of water). The lowest quantity of roots was found in the 'moist but not wet' (these plots received a total of 742 and 462 mm. of water). There was a tendency for the wetter plots to have a higher percentage of their root-weight in the upper 7·5 cm. of the soil. The percentage of the plants' weight in the roots at the end of the growing season was least under the 'moist but not wet' conditions. The results of this experiment are difficult to interpret as the weight of roots determined represents the balance between the decay of roots, most of which would be produced prior to the experimental period, and the growth of

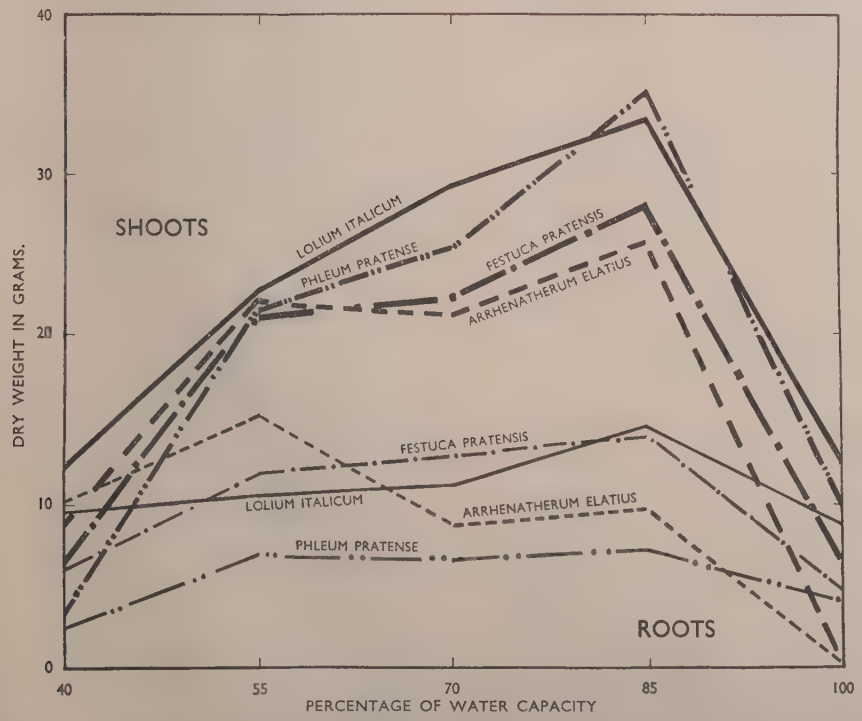


Fig. 13. Dry weight of roots and shoots of plants grown in soil kept at 40%, 55%, 70%, 85% or 100% of its water capacity. (*Kauter*, 1933)

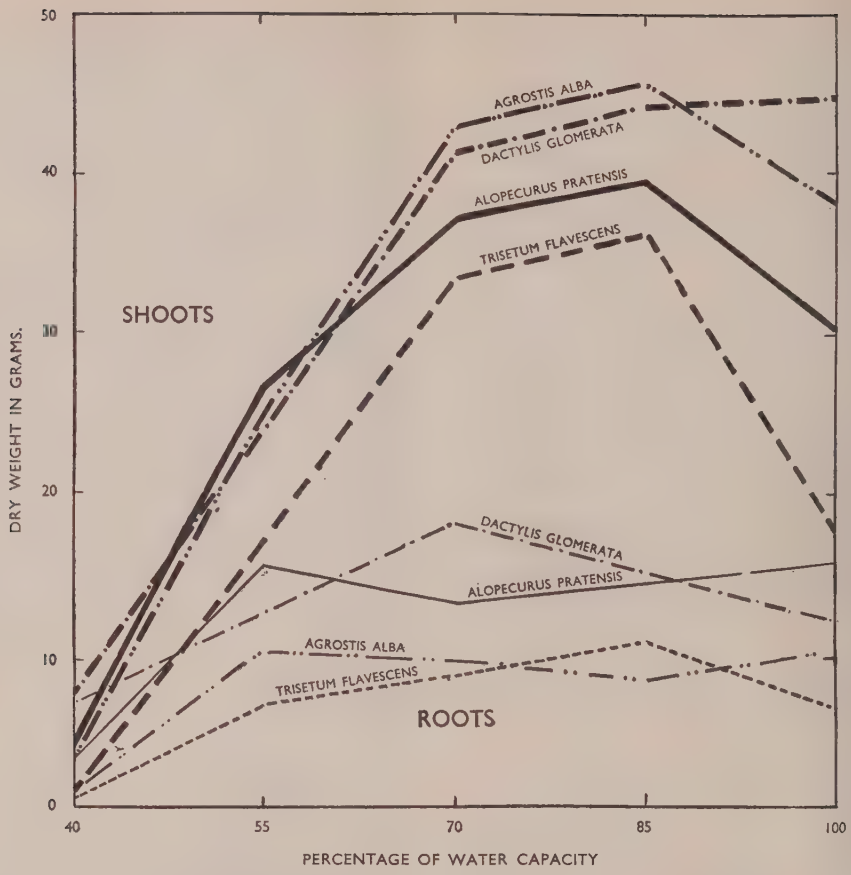


Fig. 14. Dry weight of roots and shoots of plants grown in soil kept at 40%, 55%, 70%, 85% or 100% of its water capacity. (*Kauter*, 1933)

new roots during the experimental period; also the botanical composition of the plots changed according to the treatment given.

Scarcity of Water frequently limiting Growth

The effect of insufficient water for optimum growth is shown in an experiment made by Bailey (1940). Plants of three grass species were grown in soil with a water content of 19 or 30% of its dry weight. These water contents were chosen to represent low and intermediate amounts as indicated by the wilting coefficient and moisture-holding capacity of the soil. The plants were grown under these moisture conditions for 115 days from the seedling stage. At the end of this period the plants grown with the higher water content had produced most weight of roots and shoots, the shoot growth being affected to a greater extent than the root growth by variations in the soil's water content (Table 30). Similar results were obtained by Langley and Fisher (1939) under field conditions when comparing swards composed mainly of *Bulbilis dactyloides*, with and without contour-listing of the soil, in an environment where summer growth was limited by lack of water. Contour-listing increased the soil's water content and the depth of penetration by water, and this was reflected in a greater basal ground-cover by the plants and by a greater herbage yield. The weight of roots and their depth of penetration was also increased. A high percentage of the roots on the unlisted area appeared to be dead, while

TABLE 30

Weights of dry matter in roots and shoots produced under two levels of soil moisture
(Total of 3 pots in grams)

(*Calculated from Bailey*, 1940)

Species	Soil moisture in percentage	Roots	Shoots	Percentage of plant's weight in the roots
Bromus marginatus	19	115·9	105·1	52
	30	129·0	263·7	33
Agropyron smithii	19	87·1	49·3	64
	30	290·3	183.8	61
Agropyron ciliare	19	49·1	49·8	50
	30	76·8	84·9	48

those from the listed area were in a vigorous growing condition. The percentage of the plant's weight in the roots decreased with the increased moisture content.

When plants of *Holcus sorghum* var. *sudanensis* grown together were competing for water, De Peralta (1935) and Nedrow (1937) both found that the growth of the roots and herbage per plant decreased with increasing competition (p. 116).

As a result of work in Nebraska and surrounding States under prairie conditions, Shively and Weaver (1939) stated that the amount of underground material produced by several species decreased with decreasing precipitation. Table 31 summarises the results obtained with 'upland' grasses at 5 centres. In all areas there was a significant positive correlation between root-weight and volume.

In Russia, frequent heavy furrow-irrigations (minimum soil moisture of 20–22%) were stated by Tukalova (1952) to increase the hay yield from perennial herbage, but not to affect the root-weight. Frequent light irrigations or infrequent heavy ones, accompanied by a lowering of the soil moisture to 14–15% in the intervals between the irrigations, markedly increased both the accumulation of root residues and the hay yield.

When water occurs in the deeper soil layers while the upper regions are dry, deep roots have been shown to enable the plant to utilise this water in producing shoot growth. Jacques (1941), in New Zealand, showed that the severing of the roots of *Lolium perenne* plants 12 inches from the soil surface during a dry summer resulted in the death of the plants; severance at 24 inches resulted in a severe check to the growth of the plants, and at 36 inches only a slight check. In California, Laude (1953) found that plants of *Poa scabrella*, whose roots had been cut at 2 or 4 feet below the surface, did not commence growth after their summer dormancy until after rain had fallen. Those plants whose roots had not been cut recommenced growth some weeks prior to this. Both these experiments indicate that deep roots enable plants to obtain water from a considerable depth when the upper soil layers are dry. This is in accordance with Nilsson-Leissner's (1940) findings during the selection of plants of *Trifolium repens* for drought resistance. Deep roots are, of course, only of value to the plant when water is present in the lower soil layers.

The fact that root systems developed under conditions of limited water supply are adapted in such a way as to make full use of what water is available has been commented upon by several writers. Weaver and workers of his school in particular have noticed it in the prairies near Nebraska. Some of this work is summarised by Weaver and Clements (1938). In the tall-grass prairie of eastern Kansas, Nebraska and Iowa there was sufficient rainfall to wet the soil deeply

TABLE 31

Average volume and dry weight of the underground parts of upland grassland from five areas with differing amounts of precipitation

(Weight and volume of underground parts per half square-metre)

(*Shively and Weaver*, 1939)

Area	Average precipitation per annum (in.)	Underground parts		Correlation between weight and volume
		Volume (c.c.)	Dry weight (grams)	
Anita	32·2	1221	375	+0·812
Lincoln	29·1	1027	301	+0·695
Nelson	26·2	963	272	+0·847
Phillipsburg	23·3	892	241	+0·958
Burlington*	17·4	879	249	+0·907

* Possibly better than average prairie.

but not to such an extent that aeration was impaired, while aerial conditions promoted high transpiration. Out of 43 species (not all grasses) selected as typically representative of the area, 14% had their roots almost entirely in the surface 2 feet of soil, 21% had roots extending below 2 feet but seldom below 5 feet (e.g. *Koeleria cristata*, *Elymus canadensis*, and *Stipa comata*), while 65% had roots reaching depths below 5 feet (e.g. *Andropogon* spp., *Spartina michauxiana*, and *Agropyron* spp.). Thus the roots of the above species were grouped into three more or less definite absorbing layers, many of the more deeply-rooted species having few or no absorbing roots in the first foot or two of soil.

On the hard-loam short-grass plains of western Nebraska, Kansas and eastern Colorado, because of low precipitation and high-run off only the top 18–24 in. of the soil was regularly moist. Absorption was through the minutely and profusely branched fibrous roots of the dominant short grasses (e.g. *Bouteloua gracilis*, *B. hirsuta*, *Muehlenbergia gracillima* and *Bulbilis dactyloides*) in the upper 18–24 in. of the soil. All these species were well fitted to absorb moisture vigorously following light showers because of their widely spreading shallow roots.

In mixed prairie association where the conditions were intermediate, dry soil occurred at 4–5 ft. and the roots of the 'short' grass species penetrated more deeply. The root systems of the species common to the tall-grass prairie were abbreviated in depth, this usually being correlated with the development of a more or less extensive surface absorbing system.

Soil-type in relation to water penetration was found greatly to modify the kind of vegetation within an area of equal rainfall. In eastern Colorado with a rainfall of 17 inches, typical short-grass plain conditions occurred on hard-loam soils. Where the soil became more sandy, water penetration was deeper and more deeply-rooted grasses, e.g. *Aristida purpurea*, became dominant. Where the substratum was nearly pure sand, run-off was practically nil and water penetration reached a maximum. Here the very deep-rooting grasses, e.g. *Andropogon hallii* and *A. scoparius* were dominant.

The Palouse (*Agropyron*|*Festuca*) prairie of the Pacific Northwest was found to grow under a precipitation moderate in winter and low in summer. The silt-loam soils were usually deep and had a high water-retaining power. In early summer the surface soil layers lost all their available water as indicated by the early maturing of the dominant *Festuca ovina* and certain other shallow-rooted grasses. As the season advanced, drought occurred in the deeper soil, the sub-soil usually being thoroughly depleted of its moisture. *Agropyron spicatum*, another dominant, dried out in July but renewed its growth with the advent of the autumn rains. This species made little provision for water-absorption from the surface soil, the root system penetrating to 4 feet. Many of the other species absorbed water from the first 4 to 6 feet of soil; a few penetrated more deeply. Nearly all the species matured by mid-summer, late-flowering grasses being noticeably absent.

Adaptation to the limited water supply of the prairie was stated by Blake (1935) to consist mainly of a deeply-penetrating root-system which developed rapidly after germination, the roots often having lateral branches, and the whole root-system being well developed before the shoot was exposed to transpiration. In Australia, Osborn, Wood and Paltridge (1931) noted that the root-system of *Stipa nitida* growing in arid regions consisted of a fairly compact surface-rooting portion with a more diffuse and deeper-rooting portion extending to a depth of over 40 cm. By means of this double rooting-system the plant was able to utilise the light falls of rain which wet the surface only, in addition to tapping the deeper water reserves of the soil. A similar root system was found by Goossens and Stapleberg (1933) to be formed by *Themeda triandra* in the Western Transvaal. This they also attributed to the utilisation of both light showers and the deeper soil water.

Results of experiments by Baumann and Klauss (1955) show the adaptation of plants growing in pots to their water supply. Plants of twelve grass species were grown during the summer each year in pots in which the water table was kept at 36 cm. below the surface. In a wet year it was found that the majority of species produced a greater weight of roots than in a drier year and that a greater percentage of the roots occurred in the upper 12 cm. of the soil. Evidently in a wet year the plants relied more on precipitation for their water than in a drier year when more use was made of the high water-table.

Soil-moisture depletion was noted by Rogers and Raptopoulos (1945) to occur most rapidly in

the upper 6 inches of the soil under a short-term ley, i.e. the layer that contained the greatest amount of roots. Hagan and Peterson (1953) assumed the rate of water extraction from the soil to be a measure of the root activity of swards receiving irrigation. While considering transpiration rates in Great Britain, Penman (1949, 1952) assumed that the amount of water in the soil readily available to a crop was governed primarily by the depth of the crop's root system, and only secondarily by the moisture-holding capacity of the soil and the management of the crop. The root zone concerned in the absorption of water from the soil, Penman termed the 'root constant', which for grassland he considered varied between 2 and 6 inches.

Drought

Drought is defined as dryness or a want of rain, but in practice this is frequently accompanied by high temperatures.

The effects of drought were simulated by Olmsted (1941, 1942) in experiments with seedlings of *Bouteloua curtipendula*. Under conditions which favoured the drying of the soil, seedlings were watered at intervals of 3, 6, 12 and 20 days, a standard amount of water being given on each occasion. After four months it was found that the number of living functional nodal roots varied directly with the amount of water supplied. The number of basal nodes bearing roots and the number of root primordia on the upper crown nodes to a limited degree varied inversely with the amount of water supplied. The primary root-system developed rapidly but consisted only of a single tap-root and its branches. It became non-functional within two months in most of the plants receiving water every 3 or 6 days, but was alive at the end of four months in the plants receiving water every 12 or 20 days; in some cases it was the only functional part of the root system. The nodal roots required approximately three consecutive days when the surface of the soil was wet to penetrate sufficiently to become established. A tendency was noted for a relative increase in the numbers of primordia differentiated at the upper crown nodes, and on the tillers, in those plants on which no nodal roots had become established.

In a further experiment, plants from each watering series were kept without water for 48 or 110 days, starting when the plants were 18, 30 and 42 days old. The few seedlings which failed to survive the 48-days drought, and many of the number that failed to survive for longer periods, had failed to establish nodal roots, either because of having been deprived of water prior to, or just at the time of, initiation of such roots, or because infrequent watering had prevented their establishment. A small number of plants, however, survived 48 days of drought with no established nodal roots. Initiated nodal root primordia either died or failed to grow effectively after two to three weeks of water deficit. Many root tips, established in the soil, apparently survived the drought but resumed growth very slowly when water was made available, in contrast to the stem meristems. Drought, when it prevented the establishment of adventitious roots, tended to stimulate the initiation of root primordia on the various axes after watering had been resumed. In seedlings of *Heteropogon contortus* a moderate drought was stated by Glendening (1941) to result in a decrease in both root- and shoot-growth, shoot growth being affected to a greater extent than root growth.

In established plants of *Cynodon dactylon* and *Paspalum notatum*, Burton, De Vane and Carter (1954) found that those plants with a high percentage of their roots in the lower layers of the soil (to a depth of 8 feet) were those which were most resistant to drought. Total root-weight could not be correlated with drought resistance. This is what would be expected from the work of Jacques (1941) and Laude (1953) (p. 75). These deep roots are only of value while there are reserves of water in the lower soil layers. Thus a long continued drought of several years was found by Weaver and Albertson (1943) to reduce the maximum rooting depth of *Buchloë dactyloides* and *Bouteloua gracilis* from 4–5 feet to 18 inches. The reduced rainfall during those years resulted in the soil being moistened to a much shallower depth than formerly and the reserves of water in the deeper layers becoming exhausted.

Plants of several strains of *Bromus inermis* of known drought resistance were studied by Cook (1943) during their first 6 months of life from germination, when grown with adequate moisture. This species was found to produce two types of roots (p. 9). It was concluded that measurements of the 'large' roots were a less reliable index of drought resistance than measurements of 'small' roots. Drought-resistant strains produced larger numbers of both large and small roots, greater

total axial root-lengths and greater average weight of roots and herbage, and a greater percentage of the plant's weight was in the roots. No significant difference was found in lateral spread between resistant and non-resistant strains.

Bailey (1940) endeavoured to estimate the drought resistance of three species (*Agropyron smithii*, *Agropyron ciliare* and *Bromus marginatus*) by measuring the length of time the subterranean parts would remain dormant when kept without water. The plants were grown for six weeks in soil with a moisture content of 25% of the soil's dry weight during which time the plants grew vigorously and became firmly established. The soil moisture was then reduced to 10%, the wilting coefficient being 16·2%; the foliage soon died. After six weeks, water was given to the plants and all of them renewed their growth vigorously within ten days. The soil moisture was then reduced to air dryness (4%). The tops became dry and the underground parts dormant. After five months in this state, water was given and all the plants produced new shoots. The soil was then reduced to air dryness and after another six months water was given again. Half the plants of *Agropyron smithii* resumed growth, but not very vigorously, but the plants of the other two species failed to resume growth.

Lack of water may protect plants from the ill effects of high temperature. According to Brown, E. M. (1943), in a summer with high temperatures the carbohydrate reserves of *Poa pratensis* were depleted when the plants were supplied with water, but not when they were subjected to drought. Irrigation during a drought hastened the death of the older rhizomes and the decay of the older roots.

Scarcity of Soil Water not normally limiting Growth

Excess water in a soil is manifest by too high a percentage of water in the pore-space, and possibly by a high level of the water-table, i.e. the level below which the pore space of the soil is completely filled with water.

Linkola and Tiirikka (1936) investigated the root systems under three sward types in northern European conditions. The swards were:

(1) An *Antennaria* meadow with xerophilous vegetation (*Festuca ovina*, *Antennaria* spp., and *Thuidium abietinum* association).

(2) A *Nardus* meadow with xero-mesophilous vegetation (*Nardus stricta*, *Deschampsia flexuosa* and *Pleurozium schreberi* association).

(3) An *Alchemilla* meadow with meso-hygrophilous vegetation (*Agrostis capillaris*, *Alchemilla pastoralis*, *Rhytidiadelphus squarrosus* association).

The first meadow was representative of dry conditions while the latter two were representative of 'fresh' or humid meadows. All three meadows contained a large number of species, not all grasses; about one half were common to all three. Characteristic of the humid meadows was the promotion of secondary root formation. The root lengths of most species were considerably greater in the dry meadow than in the humid ones (Table 23). In those species that exhibited the same root growth in all three situations, reduced vitality was evident in most of them in the dry meadow. Deep rooting was very common in the dry meadow while in the humid meadows shallow rooting predominated. A greater percentage of the roots, by weight, was found in the lower layers of the soil in the dry meadow than in the humid ones. The breadth of rooting varied slightly with locality. Root layering was observed in a modest form but was only clearly developed in the *Antennaria* meadow, where the depth of rooting of many species was considerable. The poor development of the subterranean layering had an analogy in the poor development of layering in the aerial shoots. (cf. Weaver and Clements, 1938) (p. 117).

After surveying German grasslands, Kmoch (1952) came to the conclusion that soil drainage was one of the major factors influencing the root-weight found beneath a sward. He found large root-weights in very wet and very dry soils, with smaller weights in intermediate soils. The percentage of roots in the upper 10 cm. was less in the very dry and very wet soils than in the intermediate ones. These results need to be considered with care since other factors, e.g. botanical composition, pH, etc., may have influenced the results, and the weights actually represent the balance between growth and decay as the swards were nearly all a year or more old.

The effect of the water content of the soil on the growth of a species native to very wet soils was studied by Weaver and Himmel (1930).

This species, *Spartina michauxiana*, was described by Weaver (1926) as having the coarsest roots of any species of grass he had examined, coarse roots being common to several species which thrive in moist situations. Weaver and Himmel stated that plants of this species grew equally well in waterlogged soil and soil which was alternatively waterlogged and drained. In dry to moist soils their growth became progressively poorer as the soils became drier. The percentage of the plant's weight in the roots was greater in the drained than in the waterlogged soil.

Weaver and Himmel emphasised the relationship between aeration and the water-content of the soil in their descriptions of the root system under the varying conditions. Response to poor aeration, i.e. high water-content, was shown by the development of a shallow root system of much-branched roots which presented a large surface in proportion to volume. Apart from this surface portion of the root system, the development of the lateral roots increased with increased aeration. Where dry soil hindered or prevented elongation, branching occurred at the root tips. Root depth increased with decreasing water content until the soil became too dry for root growth. Root hairs were few and irregularly distributed in saturated soil and became progressively more abundant as aeration increased with decreasing water content.

Level of the Water-Table

The effect upon plant growth of the depth at which the pore spaces of the soil are more or less completely filled with water was the subject of an experiment by Frankena and Goedewaagen (1942) in the Netherlands. Concrete cylinders, 100 cm. deep and 30 cm. in diameter, were filled with undisturbed cores of soil and turf from old grass fields. Cores were taken from two fields, one with a sandy and the other with a clay soil. The water level in each cylinder was then kept constant at 20, 50 or 80 cm. below the soil surface, the cylinders being 100 cm. deep. After two to three years it was found, in general, that the lower the level of the water, the greater was the root and the smaller the herbage weight. Therefore the lower the level of the water the greater was the percentage of the plant's weight in the roots. (Table 32). The increase in the weight of roots in the cylinders with the lower water-levels was relatively greater in the lower than in the upper layers of the soil, so that the cylinders with a high water-level had a higher percentage of their root-weight in the upper layers, but a lower percentage in the lower layers, than had the cylinders with a low water-level.

In another series of cylinders the water-level was maintained at 20 cm. below the surface during the winter months and at 80 cm. below the surface during the summer. These latter cylinders produced a lower weight of roots than did those in which the water-level was maintained constantly at 80 cm., but there was little difference in the weight of the herbage produced, so Goedewaagen concluded that the plants did not utilise this rise in the water-level during the winter.

TABLE 32

Effect of water-level upon the root weight (dry matter) in the sand cylinders (May/June 1940)

(*Frankena and Goedewaagen*, 1942)

Soil horizon (cm.)	Water-level depth below surface (in cm.) 80	50	20	80	50	20
	Root weight (grams)			Distribution of root weight in percentages		
0–5	18·068	14·560	16·900	79·91	90·95	79·70
5–10	1·889	0·748	2·843	8·35	4·67	13·41
10–15	1·206	0·346	0·833	5·33	2·16	3·93
15–20	0·728	0·200	0·353	3·22	1·25	1·66
20–35	0·493	0·121	0·218	2·18	0·76	1·03
35–50	0·143	0·029	0·045	0·63	0·18	0·21
50–65	0·065	0·004	0·012	0·29	0·02	0·06
65–80	0·018	0·001	0·001	0·08	0·01	+
80–100	tr.	0	tr.	+	0	+
Total	22·610	16·009	18·976			
Shoot weight (grams)	2·764	3·209	4·311			
Percentage of the plant's weight in the roots	89	83	81			

The swards used in this experiment contained several species, viz. *Lolium perenne*, *Holcus lanatus*, *Agropyron repens*, and dicotyledonous weeds. The botanical composition changed during the course of the experiment and this may have influenced the results obtained.

These results are, however, in agreement with those of Eden, Alderman, Baker, Nicholson and Firth (1951), in England, who reported that a high water-table in a fen soil reduced the depth of rooting, the lateral spread, and so the total root production of *Lolium multiflorum* after one season's growth. Likewise Osvald (1919) stated that a high water-table caused the roots of *Phleum pratense*, *Festuca pratensis* and *Poa pratensis* to concentrate in the upper layers of the soil. In Dutch Guiana, Ampson (1954) reported that there was a close correlation between the root depth of *Paspalum notatum* and *Pennisetum purpureum* and the level of the water-table, root depths being greater where the water-table was lower. The plants with the greatest root-weight were not necessarily those with the deepest roots.

Root systems of prairie plants growing in Illinois, were, in the opinion of Sperry (1935), smaller and penetrated less deeply than those of similar species growing in Nebraska, Kansas and eastern Colorado. This fact Sperry attributed to the abundant soil moisture, the relatively high water-table and the consequent deficiency of oxygen in Illinois. The percentage of the plant's weight in the roots was apparently lower in the wetter regions.

CHAPTER 15

SOIL TEMPERATURE

In general the temperature in relation to the growth of a plant shows three cardinal values. The minimum, or lowest temperature at which growth is exhibited; the optimum, or the temperature at which growth is most rapid; and the maximum, or highest temperature at which growth will take place. These values are not so definite as was once supposed but vary over a considerable range, depending upon the plant material (viz. age, part of plant, species, etc.), the period of exposure to the temperature, and other factors, (Brown, E. M., 1939; Thomas, 1947; Shaw, 1952). The whole subject of the relationship between plant growth and soil temperature has been reviewed by Shaw (1952).

Different plant species have been shown to have different optimum temperatures for root production, these temperatures differing slightly from one experiment to another. This is illustrated in Table 33, where the results are presented of several experiments in which young plants were grown at different temperature levels and their roots weighed.

The temperature at which *Poa pratensis* and *P. compressa* produced the greatest weight of herbage was found by Brown, E. M. (1939) to be higher than that at which the greatest weight of roots was produced. Kauter (1933) obtained similar results with *Lolium italicum*, *Festuca pratensis* and *Phleum pratense*; and Sprague (1943) with *Bromus inermis*. No different optima were noted in *Arrhenatherum elatius* by Kauter, in *Dactylis glomerata* by Brown, E. M. (1939), or by Sprague, V. G. (1943) in the species he studied, other than in *Bromus inermis*; or by Harrison (1934) and Darrow (1939) in any of the species they studied, the greatest weights of both root and shoot being produced at the same temperature. In these experiments the lack of difference between the optima cannot be attributed to the lack of a temperature high enough to allow the plants to develop their optimum shoot growth, although this may be the case in Kauter's results with *Alopecurus pratensis*, *Trisetum flavescens*, *Dactylis glomerata* and *Agrostis alba*, and Brown's results with *Cynodon dactylon*, where the maximum growth of shoot and root was produced at the highest temperature to which the plants were subjected. It may, however, be due to the difference between the optima being smaller than the

TABLE 33

Temperatures (°F.) at which the greatest dry weight of roots was produced

Author	Kauter (1933)	Harrison (1934)	Brown, E. M. (1939)	Darrow (1939)	Stuckey (1942)	Sprague, V. G. (1943)	Lovvorn (1945)	Mitchell (1954)
Temperatures used in the experiments	48 63 86	60 80 100	40 by 10° intervals to 100	59 73 87	50 60 80	40–55 55–70 70–85 85–100	60–70 80–90	45–55 60–70
Species	Optimum temperature							
Agrostis tenuis					60	55–70		
Agrostis alba	86							
Alopecurus pratensis	86							
Arrhenatherum elatius	63							
Axonopus affinis							80–90	
Bromus inermis						55–70		
Cynodon dactylon			100				80–90	
Dactylis glomerata	86		70			55–70		
Festuca pratensis	63					55–70		
Lolium italicum	63							
Lolium spp.								44–55
Paspalum dilatatum							80–90	
Phleum pratense	63					55–70		
Poa compressa			50					
Poa pratensis		60	60	73		55–70	60–70	
Sorghum vulgare var. *sudanense*						70–85		
Trisetum flavescens	86							

TABLE 34

Weight of shoot and root (in grams dry matter per plant) produced by plants grown at 48, 63 or 86°F. (*Kauter*, 1933)

Species	48°F.			63°F.			86°F.		
	Wt. of root	Wt. of shoot	Percentage of the plant's weight in the roots	Wt. of root	Wt. of shoot	Percentage of the plant's weight in the roots	Wt. of root	Wt. of shoot	Percentage of the plant's weight in the roots
Lolium italicum	0·30	0·74	31	1·61	6·26	20	1·40	6·41	18
Arrhenatherum elatius	0·20	0·30	40	0·74	3·38	18	0·50	2·49	17
Festuca pratensis	0·29	0·67	30	0·80	3·06	21	0·73	3·24	18
Phleum pratense	0·09	0·22	29	0·35	1·21	22	0·32	1·52	17
Alopecurus pratensis	0·14	0·23	38	0·29	1·34	18	0·38	1·43	21
Trisetum flavescens	0·09	0·06	60	0·27	0·58	32	0·28	0·80	26
Dactylis glomerata	0·24	0·53	31	0·60	2·43	20	0·66	3·00	18
Agrostis alba	0·09	0·14	39	0·17	0·60	22	0·26	1·23	17

intervals by which the temperature was increased in each experiment.

The effect of temperature on the distribution of the plant's weight between root and shoot appears to vary between experiments. In Sprague's experiment (1943), the percentage of the plant's weight in the roots increased with increasing temperature to a maximum at, or below, the temperature at which the greatest total and root dry-matter was produced. A similar trend may be detected in Brown's results. The results of Lovvorn (1945) except in *Poa pratensis*, and Kauter (1933) (with two exceptions: *Alopecurus pratensis* and *Arrhenatherum elatius*) showed that in their experiments this percentage decreased with increasing temperature, reaching a minimum at the highest temperature, which was also the temperature at which the greatest total of dry matter and root dry-matter was produced (Table 34). Mitchell (1954) found that the highest weight of both roots and shoots and percentage of the plant's weight in the roots was produced at 45–55° F. rather than at 60–70° F. (Table 37). In another experiment with *Lolium perenne*, *Dactylis glomerata* and *Paspalum dilatatum* the proportion of the plants' weight in the roots was higher in plants grown at 59°F. than at 83°F. (Mitchell, 1955). In Harrison's (1934) and Darrow's (1939) experiments no consistent trends were evident. In Kauter's experiment the number of roots produced did not always vary in the same manner as did the root weight. All species except *Phleum pratense* and *Dactylis glomerata* produced the greatest number of roots at the highest temperature; the two exceptions produced most roots at the intermediate temperature. Nor did the number of roots produced per tiller show any apparent relationship with the percentage of the plant's weight in the roots, as three species,

TABLE 35

Number of roots and shoots (tillers) per plant produced by plants grown at 48, 63 or 86°F. (*Kauter*, 1933)

Species	48°F.		63°F.		86°F.	
	No. of roots	No. of shoots	No. of roots	No. of shoots	No. of roots	No. of shoots
Lolium italicum	8·20	2·34	20·04	5·70	23·70	7·84
Arrhenatherum elatius	4·71	1·50	8·54	5·42	9·90	2·50
Festuca pratensis	7·34	1·84	13·90	3·58	15·20	4·02
Phleum pratense	8·32	1·28	11·70	2·48	9·58	1·62
Alopecurus pratensis	8·32	1·80	13·56	3·08	14·68	2·74
Trisetum flavescens	5·70	1·30	9·82	2·16	13·16	1·94
Dactylis glomerata	8·24	1·52	14·38	2·54	13·78	2·50
Agrostis alba	6·46	1·46	11·12	2·12	13·02	3·04

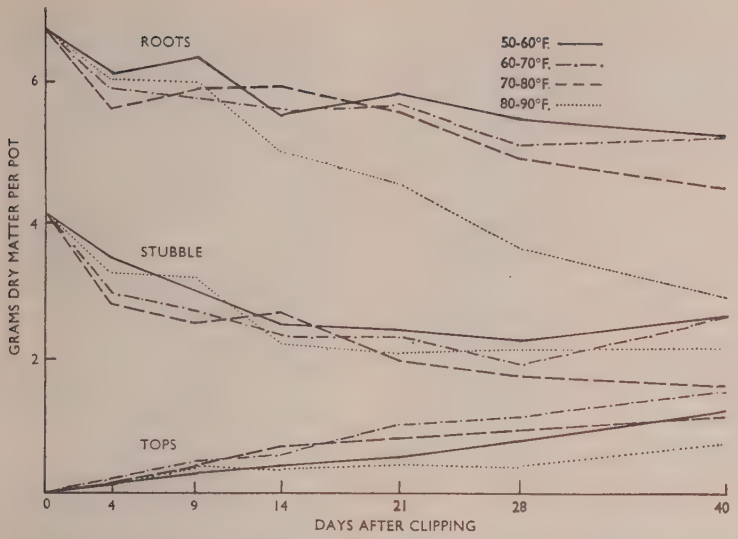


Fig. 15. Changes in the dry weights of the roots, stubble and tops of *Lolium perenne* plants at four different temperature conditions. (*Sullivan and Sprague*, 1949)

Lolium italicum, *Dactylis glomerata* and *Agrostis alba* produced the greatest number of roots per tiller at the intermediate temperature and the other species at the highest temperature (Table 35).

The reduction of root weight of *Lolium perenne* following defoliation was found by Sullivan and Sprague (1949) to be intensified by increasing temperature within the range 50–90°F. The stubble showed a similar but not so well-defined trend. The shoot weight increased least at high temperatures and most at medium temperatures. (Fig. 15). Reductions in the extent and weight of roots and in total herbage resulting from frequent defoliation were greater at 80–90° than at 60–70°F. in Lovvorn's (1945) experiment.

The time required by a root to reach maturity and the characters of a root system are influenced by soil temperature. Stuckey (1942) in Rhode Island, USA, grew seedlings of *Poa pratensis*, *Agrostis tenuis* and *Phleum pratense* in nutrient solutions held at constant temperatures. She found that the roots in the solutions held at 45°F. were healthy but only about half as long as those held at 60° F., while those held at 90° F. were dark, gnarled and had stubby black ends. Many of the plants whose roots were held at 90° F. died and all others were pale yellow. In a second experiment, seeds of *Agrostis tenuis* were germinated and grown in soil maintained at temperatures of 50, 60 and 80° F. The seeds germinated in late January and the beginning of February. On 5th April, the plants grown at the lowest temperatures had white, translucent and relatively unbranched roots, resembling those found out of doors in late March. The roots of the plants grown at 60° F. were more slender, profusely branched and longer, resembling those found out of doors during late April at the time of maximum root-growth. The roots produced at the highest temperature were less extensive, and were fine and fibrous, resembling those found in mid-summer. The tips of these high-temperature roots which were touching the bottom of the soil container were club-shaped and twisted. Lateral roots were present much nearer to the tips of the main roots of the plants grown at the lower temperatures. On 12th June, the roots from plants grown at the higher temperature were sparse and short and many of them had decayed, while the roots grown at the lowest temperature were still translucent and relatively unbranched. Stuckey concluded that the maturation of the roots was accelerated by high soil-temperature and occurred in plants grown at the highest soil-temperature before any extensive ramification of the roots had taken place. The roots grown at the lowest temperature were still

immature long after those grown at the highest temperature had disintegrated.

Observations on plants of *Poa pratensis* grown at soil temperatures of 59, 73 and 87° F. were made by Darrow (1939). After 11-weeks' growth at the highest temperature the roots were small, light brown and finely branched into a tufted dense system, whereas at 59° F. the roots were large in diameter, succulent, white, and with a few scattered laterals. High temperatures favoured rapid maturation of the roots with consequent production of laterals almost to the extreme tips of the main roots. At low temperatures more rapid elongation occurred before maturation, causing relatively long tips. The root systems at 59 and 73° F. penetrated almost twice as deeply as those produced at 87° F. In E. M. Brown's (1939) experiment high temperature reduced root production more in the lower layers of the soil than in the upper layers.

The temperature of that part of the soil lying near the surface was stated by Brown, E. M. (1939) to have a greater influence upon the growth of *Poa pratensis*, *P. compressa* and *Dactylis glomerata*, than the temperature of the soil at lower levels. A temperature of 90° F. localised in the surface layer exerted much the same effect upon root and rhizome growth as the same temperature applied to the entire root system.

When plants were exposed to variable temperatures, a high day-temperature (80 or 90°F.) was found by Brown, E. M. (1939) to exert a greater influence than a low night-temperature (50 or 60°F.) on the growth of *Poa pratensis*, *P. compressa* and *Cynodon dactylon*, but not of *Dactylis glomerata*. In the last species the two temperatures appeared to counter-balance each other. Benedict (1940) compared the effect of growing plants at a constant temperature of 75°F. and at a temperature of 75°F. during the day and 60°F. during the night, the length of day being either 10 or 18 hours. A low night-temperature increased the root weights of *Agropyron smithii* and *Andropogon furcatus* in both the long and short days, and that of *Panicum virgatum* in the short days, but decreased that of *Bouteloua gracilis* in both day-lengths and that of *Panicum virgatum* in the long days. The distribution of the plant's weight between root and shoot was unaffected by the varying temperature. Sprague, V. G. (1943) and Mitchell (1954) used variable temperatures in their experiments without comparing their effect with that of a constant temperature. The other workers mentioned in this chapter used constant temperatures so far as their equipment would allow.

The optimum temperature for the growth of rhizomes of *Poa pratensis* (Brown, E. M., 1939; Darrow, 1939; Harrison, 1934), and *Poa compressa* (Brown, E. M., 1939) is similar to that of their roots. High temperatures stimulated the emergence of the growing points of rhizomes above ground, unless the temperature was so high that growth of the rhizomes ceased (Brown, E. M., 1939; Harrison, 1934). In this connection, the application of nitrogenous fertilizer apparently has a similar effect to an increase in temperature (Harrison, 1934). After exposure to a high temperature which caused their growth to cease, rhizomes of *Poa pratensis* have been reported to start growing again from the lateral buds, but not from the terminal ones (Harrison, 1934).

The following reasons for the variations of plant growth with temperature have been put forward by Brown, E. M. (1939):

1). The reduction in the growth-rate with falling temperature below the optimum, but above the minimum, is due to the retarding effect of low temperature on water absorption, nitrogen assimilation, translocation of carbohydrates or to other factors.

2). The decrease in growth-rate with rising temperature above the optimum, but below the maximum, is conditioned by the increased respiration or other factors. The increased respiration, because it is not accompanied by a similar increase in photosynthesis, reduces the net assimilation of carbonaceous food materials or other factors. The effects of the other factors, e.g. salt accumulation, are probably indirect in the sense that it is the metabolism of the plant which is being affected.

The chemical evidence corroborates the second statement with regard to the carbonaceous material. Sullivan and Sprague (1949) showed in *Lolium perenne* that at a temperature lower than the optimum for growth, synthesised carbohydrates were stored; but at temperatures higher than the optimum they were rapidly dissipated, without having contributed to the formation of new tissue. At temperatures higher than the optimum, losses caused by defoliation were not replaced but continued to exhaustion. Similar

results were obtained by Brown, E. M. (1939) who found that the percentage of nitrogen-free extract in the roots increased at temperatures below the optimum for growth, but decreased at temperatures above the optimum. In those species which were shown to have a higher optimum temperature for shoot- than for root-growth (p. 81), the decrease in net gain of carbohydrates set in at a lower temperature in the roots than in the shoots.

CHAPTER 16

PHYSICAL CONDITIONS OF THE SOIL OTHER THAN WATER AND TEMPERATURE

Soil Aeration

Adequate oxygen is essential for all roots, and within the temperature limits for root growth, the greater the soil temperature the greater must be the concentration of soil oxygen for normal growth (Cannon, 1925).

The effect of increased aeration on plants of *Bromus inermis* growing in pots was studied by Lamba, Ahlgren and Muckenhirn (1949) by passing compressed air through the soil. The soil used was Spencer silt-loam and the treatment was given from the time the seeds were sown until the plants were 3 months old. Aeration increased the weight of roots produced in every case, the greatest increase taking place in those plants which were grown in sub-surface soil (A_2 horizon) and a somewhat lesser increase when they were being grown with sub-surface soil in the upper 4 inches of the pot and surface soil (A_1 plus A_2 horizons) in the lower 4 inches. The least increase took place when the plants were grown in surface soil, or in surface soil on top and sub-surface soil below.

The inability of a root to obtain sufficient oxygen in soil below the level of the water-table may explain why so few roots are found below this level. Weaver and Himmel (1930) largely attributed the variations in the root morphology of *Spartina michauxiana*, observed when this species was grown with different amounts of water in the soil, to changes in aeration (pp. 78–9). Changes in aeration may also account for some of the variations in growth observed in soils with different physical properties.

Soil Pore-Space

The greater the amount of pore-space in a soil, the greater the amount of water plus air in relation to the mineral particles plus organic matter, i.e. the more pore-space the less compact is the soil. Kmoch (1952) in a survey of German grasslands found that the weight of roots increased with increasing pore-space in the soil. In the American prairies, Weaver (1919) observed that root penetration, root length and the amount of root-branching were reduced when plants were growing in a compact soil. The number of branches increased when the roots from a compact soil entered an earthworm burrow. Weaver suggested that this decrease in root growth may have been due to mechanical resistance or to a change in aeration. Gist and Smith (1948) noted that the root-weight under a grass sward decreased with increasing depth, as the soil-volume weight increased. Grasses usually improve the structure, and so the porosity, of the soil in which they grow (Baver, 1948; Peterson, 1950) (pp. 125–7).

The effect of variations in compactness in layers of a soil is discussed later in this chapter.

Mechanical Analysis of the Soil

Lamba, Ahlgren and Muckenhirn (1949) grew plants of *Bromus inermis* and *Phleum pratense* in a greenhouse in pots containing either a sandy soil or a silt-loam. The plants in the sandy soil, from soon after germination until they were 45 to 68 days old, produced a greater weight of roots than did those growing in the loam. Kmoch (1952) in Germany showed that high root-weights were found under grass swards growing on sandy soils and that the root-weight decreased as the soil became heavier. In an experiment in which swards were grown on cylinders of sand or clay, Frankena and Goedewaagen (1942) found that there was a higher percentage of roots in the lower layers of the clay cylinders than in the sand cylinders.

Soil Strata

Layers of clay in a sandy soil apparently encourage the growth and branching of roots more so than the surrounding sandy soil. This has been attributed to increased moisture retention by such layers (Weaver, 1919) and to a difference in aeration (Visser, 1943). The total depth of penetration is apparently usually lessened by the presence of such strata.

Fitzpatrick and Rose (1936) studied the distribution of the roots of *Buchloë dactyloides* in non-clay-pan, semi-clay-pan and clay-pan soils. The number of roots increased in the clay-pan but decreased markedly in the poorly drained 'gray'

layer immediately above the clay-pan. The roots penetrated the dense clay-pan rather than grow round the clay-pan pillars, i.e. grow horizontally along the upper edge of the clay-pan and then vertically where the clay-pan ceased. The total depth of penetration was less in the clay-pan soils, this depth being loosely related to moisture penetration. A similar finding with regard to distribution was made by Ruby and Young (1953) under a sward of *Paspalum plicatulum*, the weight of roots in a clay-pan being twice that in the sand immediately above. The area in which this investigation was carried out occasionally suffers from drought, and Ruby and Young put forward the view that the clay-pan serves as the principal source of nutrients and water during drought periods.

Similarly, in the prairies of eastern Nebraska, Weaver (1919) noted that where the sub-soil was composed of alternate layers of sand and clay, lateral roots often occurred abundantly near the bottom of the sandy layers and in the clay stratum where the latter acted as a rather impervious layer and retained much soil moisture. Fox, Weaver and Lipps (1953), however, stated that root branching was restricted in clay-pans of certain soils in the same region, but in the soils they studied there was also a deficiency of phosphorus in the clay layers.

In the Netherlands, Visser (1943) and Goedewaagen (1943) investigated a soil profile which had compact layers at about 10–15 cm. and at 23 cm., with a much looser structure between these layers at about 20 cm. Roots were scarce in the upper compact layer, but a much greater density was observed in the loose intervening layer and also in the lower compact layer. This lower layer was very permeable, so apparently the air supply in this layer was sufficient for a strong development of roots. No abnormal twisting of the roots was observed in the compact layers. The roots did not always react distinctly to local compactness possibly owing to the influence of other, stronger, factors.

A series of soils occurs in the Netherlands in which a layer of clay overlies a sub-soil of sand. Such soils are characterised by a low level of crop production. In a study of these soils Goedewaagen *et al.* (1955) found that root concentration was high near the surface and decreased gradually with depth, but showed a definite increase near the boundary between the clay and sand, This increase was followed by a sudden diminution of the root mass in the upper layer of the sand. Only a small number of roots succeed in penetrating the sand, so that the root density in the sand sub-soil was much smaller than it was in the clay top-soil. The roots in the sand were for the greater part fleshy and poorly branched, in contrast with the roots in the clay which had a normal appearance and branched more profusely. The working depth of the root system therefore varied with the depth of the clay and the best grass crop was observed on the field with the thickest clay layer. The sandy layer was found to be generally more compact than the clay top-soil and this was thought to be the main cause of the low root concentration in this layer. In soils with a layer of clay overlying peat it was similarly noted that most of the root system occurred in the clay, very few roots penetrating into the peat. In British Somaliland, Glover (1951) noted, in certain deep alluvial sandy soils, that wherever a layer of heavier or more clayey soil appeared, the grasses showed a more intensified development of secondary lateral roots and rootlets. These layers were always moister than the looser, coarser layers.

CHAPTER 17

HYDROGEN-ION CONCENTRATION OF THE GROWTH MEDIUM

Over a period of weeks, the growth of plants of *Agrostis tenuis* in sand culture using nutrient solutions of pH 4·5 and 6·5 was studied by Sprague, H. B. (1934). The greater weight of roots and stubble was produced at pH 4·5, but the greater weight of shoots and of total plant material was produced at pH 6·5 so the highest percentage of the plant's weight in the roots was recorded at the lower pH (Table 51). According to Darrow (1939), plants of *Poa pratensis* grown in sand culture were unaffected by the pH of the watering solutions within the range 4·5 to 6·5 when the nitrogen was present in the form of nitrates. When the nitrogen was present as ammonium ions the root weight increased and the percentage of the plant's weight in the roots decreased as the pH increased (Table 52).

Investigators concerned with plants growing in soil have reported that the weight of roots increased as the pH decreased from neutrality. Plants in soil were usually allowed to grow for a longer period than those grown in culture solutions, and so, in the soil experiments, the variations in pH may have affected not only the rate of growth but also the rate of decay of the old roots, the lower the pH the slower the rate of decay (p. 122). This latter influence is particularly important in experiments lasting for more than one year.

McNeur (1953) varied the pH of a soil by treatment with sulphuric acid, after which he grew plants of *Lolium* spp. and *Dactylis glomerata* in it for a year. At the end of this period, the general trend was for the total weight of roots to increase as the soil became more acid (Table 36). A regression analysis of treatment totals gave a highly significant value for the linearity of this trend. This was in contrast with the situation found in the herbage where there was a significant curved regression. It is possible that the increase in root weight in the acid soils may have been due to the lack of decomposition at the low pH levels. Much finer rootlets were produced in the more acid soils than in the other soils.

By applying fertilizers, Sprague, H. B. (1933) altered the pH of the soil growing swards of *Agrostis* spp., and after 5 years it was found that the fertilizer treatments which had lowered the soil pH to 5·5 or below were associated with a high root-weight and a sward of low vigour. Many of the roots appeared brown and non-functional. Sprague was of the opinion that these roots had accumulated from previous years because conditions were unfavourable for decay. Correlating the weight of roots and the soil pH of *Poa pratensis* swards, Haynes (1943) found a slight negative correlation within a pH range of 6·5–5·3. As a result of intensive nitrogenous fertilization with calcium nitrate, Olofsson (1941) stated that over a period of years the soil pH was increased and the root mass decreased. This was accompanied by a decrease in the prevalence of *Taraxacum officinale* and an increase in that of *Poa pratensis*, so that the increase in root mass may not be entirely due to the direct pH effect.

The previous experiments were each concerned with one soil type in a small area. In a survey of 150 German grass fields covering a wide area, Kmoch (1952) found that the root weight increased as the soil pH decreased, the pH range studied being from 4·1 to above 7·5. This variation may not have been entirely due to the direct effect of pH as to other factors, e.g. soil phosphate requirement and botanical composition of swards, tend to vary with the pH.

TABLE 36

Mean weight (grams dry matter) per six plants of roots and shoots of plants of *Lolium* spp. and *Dactylis glomerata* after 12 months growth in soils with different pH values

(*McNeur*, 1953)

Soil pH:–	7·2	6·75	5·95	4·5	3·6
Weight of shoot (grams)	63·7	68·3	69·3	71·9	62 0
Weight of root (grams)	33·3	36·4	40·4	48·9	60·7
Percentage of plant's weight in the roots	34	35	37	41	49

CHAPTER 18

LIGHT RECEIVED BY THE SHOOT

Without light, under otherwise normal conditions, a plant is unable to grow. Following partial defoliation the percentage of water-soluble carbohydrates (including glucose, fructose, sucrose and fructosans) in the roots and stubble of *Lolium perenne* plants was found by Sullivan and Sprague (1943) to decrease rapidly for several days. After approximately 11 days, carbohydrates started to accumulate in the roots and stubble of plants in the light, but in plants placed in darkness after defoliation the soluble carbohydrates continued to decrease almost to the point of exhaustion. There was also marked hydrolysis of proteins in the plants placed in the dark, an accumulation of nitrates taking place which disappeared when the plant was dying. A high temperature had a similar effect upon the plants, except that no accumulation of nitrates took place (Sullivan and Sprague, 1949) (p. 68).

The amount of light to which a plant is subjected may be varied by varying the length of the photoperiod, or by varying the intensity either directly by artificial lighting or indirectly by shading. Increasing either the length of the photoperiod or the intensity of the light apparently usually increases the growth of the whole plant, the root system being affected to a greater extent than the shoot.

Intensity

An interesting experiment was reported by Mitchell (1954). Plants of *Lolium* spp. (short-rotation ryegrass and S.23) were grown under two intensities of light, 700 and 2000 foot-candles, for ten hours per day and at two temperature conditions, a mean of 50°F. (55° by day and 45° by night) and a mean of 65°F. (70° by day and 60° by night). The plants were harvested when they had reached the same physiological growth-stage (8th leaf on the main stem), which occurred at different times after the plants had been placed under the controlled conditions (Table 37). Most root- and shoot-growth was produced under the 2000 foot-candles at 50°F., and the least under 700 foot-candles at 65°F. The percentage of the plant's weight in the roots varied directly with the total weight of material produced. This experiment differs from most others in that the plants were harvested not after a constant period of time, but when they had reached a given physiological stage of development.

Shade

Shading a grass plant from full sunlight reduces both its total growth and its root growth. Slight shade may increase the top growth but more shade certainly reduces it. Under natural conditions, shading a plant probably alters the temperature as well as the light regime, but it is very difficult to separate these two factors.

Some of the earliest experiments reported are those of Reid (1933b) who subjected plants of *Agrostis canina* and *A. palustris* to varying degrees of shade at various times of the day. Total plant- and root-growth (weight increase) were reduced

TABLE 37

Dry weight of plants of *Lolium* spp. at the same growth stage but grown in different environments (*Mitchell*, 1954)

Light intensity (ft.-candles)	Temperature (°F.)	Strain	Period under constant conditions (days)	Final weight				Percentage of plant's weight in the roots
				Leaves (mg.)	Stems (mg.)	Root (mg.)	Total (mg.)	
700	50	SR	44	95	58	27	180	15
		S.23	44	93	72	28	193	14
700	65	SR	38	79	35	15	129	12
		S.23	38	48	28	9	85	11
2000	50	SR	42	404	281	170	855	20
		S.23	48	241	179	101	521	19
2000	65	SR	24	324	176	80	580	14
		S.23	29	280	189	83	552	15

by shading; slight shading caused a slight increase in top growth, but severe shading reduced it. The percentage of the plant's weight in the roots tended to decrease with the degree of shading, i.e. the root growth was more affected by shading than the shoot growth. These observations were extended by Benedict (1941a) who found that both root- and shoot-weights produced by plants of *Agropyron cristatum*, *A. smithii* and *Bouteloua gracilis* varied directly with the degree of shade in which they were grown. The distribution of weight between shoot and root showed no distinct trends. The shading varied from 28 to 70% of full sunlight. The treatments were given to the plants for four months from the time of sowing. In later work, Mitchell (1954) (Table 43) found that shaded (38% of normal light) plants of *Lolium* spp. made much less gain in weight than those receiving full light and that the root growth was more severely affected than the shoot growth (cf. Reid, 1933b). This also occurred when the shading was decreased to 65% of normal light. The number of tillers was also reduced (Mitchell and Coles, 1955). In another experiment, Mitchell (1955) found that shaded plants of *Lolium perenne*, *Dactylis glomerata* and *Paspalum dilatatum* had a lower proportion of their weight in the roots than had unshaded plants.

Defoliation had a similar effect to shade in Mitchell's 1954 experiment (Table 44). Shading and defoliation combined thus had a two-fold effect in reducing growth and increasing the proportion of shoot to root.

An interaction between shading and nitrogen was shown by the experiments of Watkins (1940) on established plants of *Bromus inermis*. Shading (the plants receiving approximately 7% of full sunlight) greatly reduced the weight of root, rhizomes and stubble produced, but only slightly affected the weight of the hay crop. Chemical analysis showed that shading had little effect upon the composition of the roots, except in reducing their sugar content. In the hay, stubble and rhizomes, however, it decreased the percentage of the carbohydrates and increased the percentage of nitrogen. Watkins concluded that shading resulted in the carbohydrate reserves in the rhizomes and the carbohydrates produced by the plant being utilised in the production of top growth. Nitrogen fertilization had a similar effect to shade upon the distribution of the plant's weight between root and shoot, but increased the weight of hay and stubble produced. A combination of shade and nitrogen fertilizer decreased the percentage of the plant's weight in the roots and the weight of root to a greater degree than either factor alone (Table 38). The decrease in the percentage of carbohydrates in the rhizomes, stubble and hay caused by shade was accentuated by the application of nitrogenous fertilizer. The effects of shade appear, to some extent, to be complementary to those of additional nitrogen nutrition.

TABLE 38

Effect of shade and nitrogenous fertilizer treatments on plants of *Bromus inermis*. Yield in pounds dry weight per acre from harvests made in 1938. Shading treatments started March 24th, 1938

(*Watkins*, 1940)

Treatment	Plant Part				
	Hay	Stubble	Roots	Rhizomes	Total
	July 25th harvest. 1937 seeding				
Control	1,300	1,550	1,370	80	4,300
N-fertilized	5,890	2,590	1,540	50	10,070
Shaded	1,180	440	350	5	1,975
	July 5th harvest. 1936 seeding				
Control	2,170	3,280	3,400	340	9,190
N-fertilized	4,930	2,950	2,940	240	11,060
Shaded	2,580	1,290	1,580	70	5,520
N-fertilized-Shaded	2,970	1,850	1,410	70	6,300
	August 2nd harvest. 1937 seeding				
Control	1,730	1,030	2,570	90	5,420
N-fertilized	6,930	2,110	2,370	60	11,470
Shaded	1,460	360	280	15	2,115

The reduction of light available to a plant by competition from another plant of the same species was stated by Nedrow (1937) to cause a reduction of the weight of roots produced and a decrease in the percentage of the plant's weight in the roots (p. 116).

When plants of *Dactylis glomerata* and *Festuca pratensis* were kept in a greenhouse at 65°F., Hill and Carnahan (1954) found that the cloudiness of the sky had little effect upon mitotic activity in the root tips. When the plants were kept at 75°F., the root tips collected on cloudy days exhibited more metaphase cells than those collected on sunny days.

Length of the Photoperiod

With plants of many species an increase in the length of the photoperiod, at least to a certain limit, increases the weight, but not necessarily the number, of roots produced per plant, and also decreases the percentage of the plant's weight in the roots.

Watkins (1940) studied the growth of *Bromus inermis* with short (8·5 hours), normal (in Ohio) and long (18 hours) periods of illumination, the experimental treatments being given to established plants from 2nd April to 28th July. At the end of this period the weight of roots and stubble that had been produced was smallest in the plants with the short photoperiod and equal in the normal and long-period plants. The weight of hay and rhizomes produced increased with both increases in photoperiod (Table 39). Watkins stated that it

TABLE 39

Effect of length of day on *Bromus inermis* plants. Yield in lb. dry matter per acre on July 28th (*Watkins*, 1940)

	Yield in lb. dry matter per acre Treatment		
Plant part	Short day	Normal day	Long day
Hay	1780	2520	4780
Stubble	870	1380	1310
Roots	500	910	910
Rhizomes	70	230	400
Total	3220	5040	7400

appeared that length of day was important for maximum production of fertile shoots and rhizomes, most fertile shoots being produced under a normal length of day. After a certain length of day was exceeded the additional carbohydrates produced by photosynthesis were used in the growth, in size and length, of the vegetative parts.

Plants of six species of the genera *Bouteloua* were grown by Olmsted (1943) with 8-, 12- and 16-hour daylengths from the time of sowing. The species concerned were *B. curtipendula*, *B. filiformis*, *B. hirsuta*, *B. rothrockii*, *B. eriopoda* and *B. gracilis*. After five months there was a positive correlation between the dry weight of roots that had been produced and the length of day. The percentage distribution of the weight of the plant between root and shoot showed no consistent trend. The numbers of crown roots were higher in plants of five species grown with a shorter than the 16-hour day, although not significantly so, except in the case of *B. curtipendula* and *B. gracilis*. In *B. eriopoda* the numbers produced under the 8- and 16-hour daylengths were approximately equal. The value of the ratio

$$\frac{\text{number of elongated stems}}{\text{number of roots}}$$

was inversely correlated with the daylength, chiefly owing to a strong inverse correlation between the number of stems and the daylength. The results obtained indicated that the greatest numbers of root primordia per tiller were initiated with the long photoperiods, a condition probably connected with the greater numbers of basal nodes and internodes per tiller which matured before the tillers elongated.

Four species of different genera were studied by Benedict (1940) whose results showed that, after four months, plants of *Andropogon furcatus*, *Bouteloua gracilis* and *Panicum virgatum* growing with a photoperiod of twenty hours produced a greater dry weight of roots than plants growing with an eight-hour period. Plants of *Agropyron smithii* were unaffected by daylength. The percentage of the weight in the roots was less in plants of *Andropogon furcatus* and *Panicum virgatum* grown with the 20-hour photoperiods, this percentage in the other two species being unaffected by daylength. There was no apparent correlation between the length of day required for flowering and the production of dry weight.

Sprague, V. G. (1943) grew six species of temperate grasses (*Dactylis glomerata*, *Festuca pratensis*, *Bromus inermis*, *Phleum pratense*, *Poa pratensis* and *Agrostis tenuis*) and *Sorghum vulgare*

var. *sudanense* with 9- and 16-hour daylengths for six weeks after emergence. Plants grown at temperatures from 40° to 85°F. in every case produced a greater weight of roots with the longer daylength. The plants grown with the longer daylength had a lesser percentage of their weight in the roots than had those with the shorter daylength. Sprague, however, stated that the evidence was insufficient to conclude these were solely photoperiodic responses. Plants of the temperate species, except those of *Poa pratensis* and *Agrostis tenuis*, growing at a temperature of 85–100°F. apparently made more growth or lived longer with the shorter photoperiod. *Poa pratensis* and *Agrostis tenuis* made no growth at this temperature. *Sorghum vulgare* var. *sudanense* grew better with the longer photoperiod at all temperatures. The optimum temperature for the root growth of the temperate grasses was 55–70°F. and for *Sorghum vulgare* var. *sudanense*, 70–85°F.

There is also a suggestion of an interaction between the length of the photoperiod and the temperature in the results of Lovvorn (1945) (Table 40). Established plants of *Paspalum dilatatum*, *Axonopus affinis*, *Poa pratensis* and *Cynodon dactylon* were grown for two months with 10- and 15-hour photoperiods at temperatures of 60–70°F. and 80–90°F. At the low temperature level, all species, except *Poa pratensis*, produced their greatest weight of roots with the long photoperiod. At the high-temperature level, *Poa pratensis* and *Cynodon dactylon* produced their greatest root-weight with the short photoperiod, the difference being particularly marked in the plants receiving complete fertilizer. *Paspalum dilatatum* and *Axonopus affinis* both showed a slight suggestion of a third-order interaction: photoperiod × temperature × application of complete fertilizer. With fertilizers at both temperatures and without fertilizer at the lower temperature both species produced their greatest root weight with the longer photoperiod; without fertilizer at the higher temperature most weight was produced with the shorter photoperiod. At both temperatures the plants grown with the short photoperiod had a higher percentage of their weight in the roots than had those grown with the long photoperiod, the difference being most marked in the plants at the lower temperatures. In Table 40 it should be noted that comparisons for daylength effects can only be made between plants grown in 1942.

As a result of experiments not specifically designed to test its influence, Brown, E. M. (1939) stated that the length of the photoperiod had little effect upon root production by *Poa pratensis*, *P. compressa*, *Dactylis glomerata* and *Cynodon dactylon*. This is not in agreement with the conclusions of other workers as a result of more carefully controlled experiments.

The growth of rhizomes is considerably influenced by the length of the photoperiod. In Watkins' (1940) experiment, the weight of rhizomes produced by *Bromus inermis* increased with the increasing length of day. The greatest number of rhizomes was, however, produced with the normal daylength. Both Brown, E. M. (1939)

TABLE 40

The effect of soil-fertility level, temperature, and length of day on root growth by plants whose herbage was cut every 30 days. Grams dry-matter per pot

(*Lovvorn*, 1945)

Species	High temperature 80–90°F.			Low temperature 60-70°F.		
	Long day	Short day		Long day	Short day	
	1942	1942	1943	1942	1942	1943
	High fertility level					
Paspalum dilatatum	3·80	3·38	5·98	2·47	2·00	3·62
Axonopus affinis	1·18	1·15	2·20	1·45	1·06	0·64
Cynodon dactylon	1·28	2·11	2·04	1·08	0·95	0·99
Poa pratensis	1·28	1·36	0·59	3·08	3·00	2·92
Average	1·88	2·00	2·70	2·02	1·75	2·04
	Low fertility level					
Paspalum dilatatum	1·64	2·01	3·18	1·40	1·28	1·41
Axonopus affinis	1·48	1·59	1·86	0·81	0·68	0·80
Cynodon dactylon	1·34	1·49	1·36	0·67	0·57	0·59
Poa pratensis	0·89	0·92	0·45	1·25	1·36	2·07
Average	1·34	1·50	1·71	1·03	0·98	1·22

and Evans and Watkins (1939) noted that the development of rhizomes by plants of *Poa pratensis* was favoured by long photoperiods such as those provided by the days of summer, while rhizome development by plants of *P. compressa* was favoured by shorter periods, such as those provided by the days of late autumn, winter and early spring. Brown also noted that both species required relatively high temperatures before the rhizomes would emerge above the level of the soil, and that in the case of *P. compressa*, the rhizomes tended to remain below ground so long as the temperature was below 50°F. and the days were short. The observations of Harrison (1934) do not appear to be in agreement with those of Brown. Harrison stated that the rhizomes of *Poa pratensis* produced during the bright, cool days of spring, early summer and autumn by plants continuously supplied with nitrogen in the growth media, gradually emerged into the light as the short cloudy days of late autumn and winter arrived. By limiting the nitrogen or increasing the light these rhizomes not only remained below the soil level but also became stockier and new rhizomes were also produced. The reason for this discrepancy is not immediately obvious but may be concerned with the locality in which the observations were made, Brown working in Missouri and Harrison in Chicago.

CHAPTER 19

DEFOLIATION

The immediate effect of a partial or complete removal of a plant's active shoot tissue is a transference of reserves from the roots and other storage organs to the remaining shoot tissue so that it may rapidly produce new growth. This results in a loss in weight of the underground organs. This is shown in experiments of Sullivan and Sprague (1943) with *Lolium perenne* (Fig. 16) and *Dactylis glomerata* (1953).

This loss in weight by the roots and other underground organs is relatively small, the main effect of defoliation on these organs being the retardation of their growth for some time afterwards. Thus the growth in length of roots has been shown to be reduced by a single defoliation (Parker and Sampson, 1931) (Table 41). Crider (1955) has shown that the apical growth of the roots of several species was stopped completely within 24 hours or so of the removal of 40% or more of the foliage in one operation; the length of time before growth was re-started and the number of roots not recommencing growth varied directly with the percentage of the foliage removed. Under the conditions of Crider's experiment, apical

TABLE 41

Effect of defoliation on the subsequent growth in length of the root system

(Length of roots in mm. after a single removal of herbage on December 7th. Seeds sown November 23rd)

(*Parker and Sampson*, 1931)

Date of measurement	Length of root system (mm.) *Stipa pulchra* Defoliated plant	*Stipa pulchra* Control	*Bromus hordeaceus* Defoliated plant	*Bromus hordeaceus* Control
December 7	0·9	1·0	1·3	1·3
,, 8	1·0	3·1	1·4	2·2
,, 9	1·0	4·8	1·4	3·7
,, 10	1·0	5·4	1·4	5·3
,, 11	1·0	6·6	1·4	7·2
,, 12	1·0	7·5	1·4	8·7
,, 13	1·0	8·8	1·7	9·2
,, 14	1·0	9·7	1·8	10·6
,, 15	1·0	10·7	2·4	12·3
,, 16	1·0	11·9	2·8	14·2
,, 17	1·1	13·0	3·8	17·7
,, 18	1·1	14·2	4·7	19·2
,, 19	1·2	15·3	5·8	21·3
,, 20	1·2	16·4	6·5	23·2
,, 21	1·3	18·1	9·2	25·7

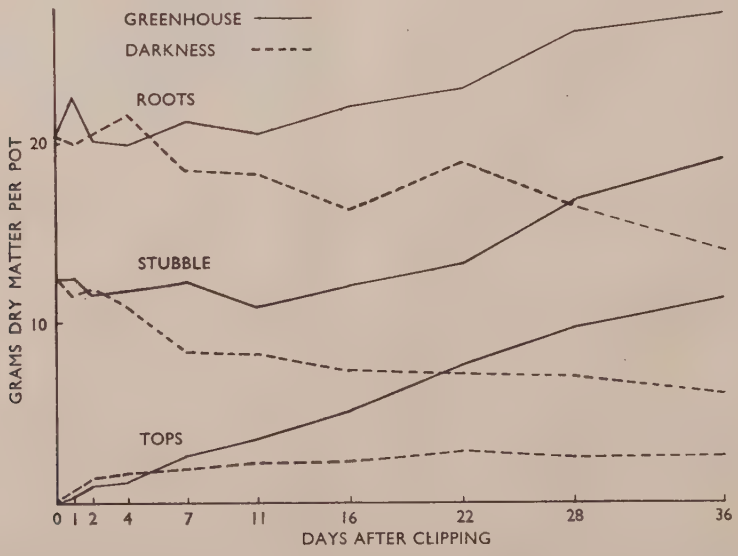


Fig. 16. Yield of roots, stubble and new top-growth of *Lolium perenne* plants growing in the greenhouse and in darkness for 36 days after removal of the tops. (*Sullivan and Sprague*. 1943)

TABLE 42

Effect of clipping the herbage on the roots of *Holcus sorghum sudanensis* plants (*De Peralta*, 1935)

	Height of cut		
	Control	6in.	2in.
	After 3 cuts		
Depth of penetration (inches)	68	58	51
Lateral spread (inches)	23	20	20
Depth of living root tips (feet)	6	4	2–3
Diameter of roots (mm.)	1·24	—	0·78
Diameter of stele (mm.)	0·662	—	0·320
Number of main roots	27	16	14
	After 4 cuts		
Weight of roots (grams)	3·23	2·39	0·68
Volume of roots (cc.)	17·0	13·0	6·0

growth was not stopped by the removal of less than 40% of the foliage. Single tillers and parts of the plants were found to act independently of the rest of the plant in this reaction to defoliation i.e. if only one tiller was defoliated then only the roots belonging to that tiller ceased apical growth. This last observation was the result of experiments with two species, *Eragrostis curvula* and *Tripsacum dactyloides*.

The number of roots initiated by a plant is also reduced by defoliation treatments, the reduction being in proportion to the severity of the treatment (Jacques and Edmond, 1952) (p. 103). The roots of defoliated plants have also been shown to be of smaller diameter than those of undefoliated plants (Biswell and Weaver, 1933; Robertson, 1933; De Peralta, 1935) (Table 42). Reference to the effect of defoliation on the anatomy of roots is made on pp. 17–18.

Following defoliation, the growth of the whole plant is reduced, that of the roots being decreased to a greater extent than that of the shoot, the difference between the growth of the root and shoot decreasing as the plant recovers from the defoliation. This is shown in the results of Mitchell (1954) with *Lolium* spp. (short-rotation ryegrass and S23) (Tables 43 and 44).

Defoliation decreases the life of roots (Weaver and Zink, 1946b) (p. 37). Certain observers have reported that the roots of defoliated plants die back from the tips (e.g. Robertson, 1933; De Peralta, 1935).

If a plant is defoliated again before it has recovered from a previous defoliation the effects of the two defoliations are combined. The accumulated effect of too many defoliations results in the death of the plant. The more severe the treatment, the sooner the plant dies (Roberts and Hunt, 1936) (Table 45). Almost any defoliation treatment 'weakens' a plant and makes it more susceptible to adverse environmental conditions.

The relative effect that defoliation treatments have upon a plant depends upon their relative severities, i.e. the proportion of the shoot that is removed, the number of times the treatment is carried out and the length of the interval between each operation, as well as upon the physiological

TABLE 43

Percentage distribution of dry-matter increment in plants of *Lolium* spp. during successive nine-day intervals after defoliation and applications of differences in light intensity (*Mitchell*, 1954)

Time	Open (100% light)			Shaded (38% light)		
	Leaves	Stems	Roots	Leaves	Stems	Roots
	%	%	%	%	%	%
0–9 days	70	22	8	86	8	6
9–18 days	51	22	27	73	17	10
18–27 days	42	23	35	60	29	11

TABLE 44

Percentage distribution of dry-matter increment in plants of *Lolium* spp. during the nine-day period following application of treatment differences outlined

(*Mitchell*, 1954)

Defoliation treatment	Light	Total dry-matter increase per plant (mg.)	Percentage distribution		
			Leaves %	Leaf bases %	Roots %
Not defoliated	Open (100% light)	77·2	43	22	35
	Shaded (38% light)	35·6	59	23	18
Defoliated	Open (100% light)	17·5	70	22	8
	Shaded (38% light)	12·7	86	8	6

state of the plant and the suitability of the environment for growth. The more severe the defoliation treatment, the greater its effect. The proportion of shoot removed has usually been controlled by experimenters by varying either the height from the ground above which all herbage was removed or the number of times a plant was defoliated in a given period.

The effect of different frequencies of defoliation has been the subject of a large number of investigations. The usual form of experiment has been to clip the shoot to a standard height a varying number of times during the experimental period and then to weigh the roots at the end of this period. Almost invariably the plants clipped most frequently had the lowest root-weight and

TABLE 45

Weight of total shoot production and weight of roots of plants subjected to seven defoliation treatments and weight of roots expressed as a percentage of shoot plus root weight (wt. in grams dry matter)

(*Extracted and calculated from Roberts and Hunt*, 1936)

	Height of cut in in.:—			1			0·5			Ground level		
	Shoots	Roots	% of the total weight in the roots	Shoots	Roots	% of the total weight in the roots	Shoots	Roots	% of the total weight in the roots	Shoots	Roots	% of the total weight in the roots
						Lolium perenne						
Date		Control							10–day interval			
9:4:34	0·259	0·354	58	0·150	0·354	70	0·207	0·354	63	0·227	0·354	61
8:6:34	17·1	12·050	41	0·789	0·080	9	0·605	0·050	8	0·297	—	
7:8:34	Not recorded	14·600		0·886	0·043	5	0·659	0·029	4		Dead	
6:10:34	26·5	4·400	14		Dead			Dead				
5:11:34		Not recorded										
3:2:35	37·85	25·49	40									
									30–day interval			
9:4:34				0·159	0·354	69	0·212	0·354	63	0·207	0·354	63
8:6:34				4·407	1·14	21	2·585	0·310	11	1·441	0·440	23
7:8:34				9·847	5·52	36	4·798	1·049	18	1·751	0·146	8
6:10:34				14·213	2·30	14	6·096	0·520	8	1·833	Not recorded	
5:11:34				15·204	1·37	8	6·216	0·940	13	1·849	0·045	2
3:2:35				15·494	0·874	5		Dead			Dead	
						Phleum pratense						
Date		Control							10–day interval			
9:4:34	0·012	0·026	68	0·012	0·026	68	0·019	0·026	58	0·024	0·026	52
8:6:34	1·78	0·36	17	0·147	0·050	25	0·086	0·140	62	—	0·010	
7:8:34	Not recorded	3·026		0·202	0·033	14	0·126	—			Dead	
6:10:34	39·15	2·550	6	0·213	0·024	10	0·140	0·010	7			
5:11:34		Not recorded			Dead			Dead				
3:2:35	33·1	3·750	10									
									30–day interval			
9:4:34				0·012	0·026	68	0·015	0·026	63	0·022	0·026	54
8:6:34				0·730	0·37	34	0·790	0·130	14	0·150	0·020	12
7:8:34				2·583	0·949	27	1·824	0·458	20	0·246	0·100	29
6:10:34				3·459	0·320	8	2·018	0·160	7	0·280		
5:11:34				3·581	0·270	7	2·049	0·060	3	0·281		
3:2:35				3·728	0·110	3	2·064	0·040	2		Dead	

— Too small for measurement

those clipped least the highest root-weight, the greater the difference in the frequencies the greater the difference in root-weights. In the many experiments of this kind which have been carried out, a large number of species, frequencies of defoliation, and lengths of time over which the treatments extended (days to years) have been investigated (Kraus, 1911; Stapledon, 1924; Sampson and Malmsten, 1926; Stapledon and Beddows, 1926; Graber, Nelson, Leukel and Albert, 1927; Stapledon and Milton, 1930, (Table 53); Graber, 1931; Biswell and Weaver, 1933; Sprague, H. B., 1933; De Peralta, 1935; Gernert, 1936; Jacques, 1937a; Klapp, 1942, 1943; Weinmann, 1943, 1944 (Table 54) 1949; Lovvorn, 1944, 1945; Crider, 1945; Carter and Law, 1948; Kennedy and Russell, 1948; Thaine and Heinrichs, 1951; Albertson, Riegel and Launchbaugh, 1953; Ruby and Young, 1953; Thaine, 1954).

The proportion of shoot growth removed at each clipping has also been the subject of several investigations. In these experiments the plants were usually all clipped at the same time, but the height at which the herbage was cut varied and the weight of roots was determined after a given number of defoliations. The results of all the experiments are nearly unanimous in showing that the lower the cut, (i.e. the greater the proportion of the shoot removed) the greater was the decrease in the weight of root, compared with the control (Roberts and Hunt, 1936 (Table 45); Hughes, 1937; Torstensson, 1938; Jacques and Edmond, 1952).

The two variables, frequency of defoliation and height of cut, are complementary, a decrease in the severity of one serving to offset an increase in the severity of the other. Many combinations of severities of these two factors are possible (*vide* Roberts and Hunt, 1936; Torstensson, 1938). In most experiments, height of cutting had a greater influence than frequency.

If the defoliation is drastic enough it will completely overwhelm any seasonal variation (Roberts and Hunt, 1936). It would be expected from the work on seasonal variation and the work of Jones (1933a, b, c and d) concerning the changes in the botanical composition of swards brought about by grazing at different times, that plants would be particularly susceptible to defoliation at certain growth stages. Klapp (1937a) was of the opinion that a plant was particularly susceptible to defoliation when complete mobilisation of reserves had taken place, which, he thought, was when there was the greatest development of fertile tillers and when regenerative buds were being formed. There does not appear, however, to be very much experimental evidence upon this point.

Partial defoliation by grazing has a similar effect to partial defoliation by clipping. Provided that the proportion of shoot removed by each method is the same, the chief differences will be due to the consolidation of the soil and the scattering of dung and urine on the sward by the animals. Some authorities (Boeker, 1954; Low, 1955) have stated that, in their opinion, grazing animals consolidate the soil to the detriment of root growth. Klapp (1943) found no difference between the root weights of swards which had been either cut or grazed once weekly for some time. In several investigations the weight of roots at the end of the experimental period has been shown to decrease with the severity of the grazing treatment. (Jones, 1933a; Wallin, 1935; Hanson and Stoddart, 1940; Weaver and Albertson, 1943; Weinmann, 1948c; Weaver, 1950).

Torstensson (1938) endeavoured to simulate 'rapid' grazing by cutting *Lolium italicum* plants to a height of 2 cm. in one cut and 'slow' grazing by gradually reducing the herbage to this height by means of a series of cuts over a period of days. In general the 'slow' grazing resulted in a lower root weight at the end of the experiment than the 'rapid' grazing. In the field, Haynes (1943) did not find any difference in the root-weights of swards of *Poa pratensis* which were grazed continuously and those rotationally grazed. *P. pratensis* is, however, relatively resistant to injury by grazing (p. 100 *et seq.*).

In an experiment with *Lolium perenne* and *Dactylis glomerata*, Jacques (1937a) found that the number of roots, as well as the weight of roots per plant, at the end of the experiment decreased in proportion to the severity of defoliation to which the plants had been subjected. The weight of roots decreased to a greater extent than their number, so that the weight of each individual root must have decreased. Albertson, Riegel and Launchbaugh (1953) found that heavy clipping reduced the number of roots of prairie species at depths of 4 and 8 inches but that moderate clipping increased their number. All clipping treatments reduced the root weight, in proportion

to their severity. The reason for the variations in root numbers is not clear.

The volume of roots at the end of the experimental period has been found by several investigators to decrease in proportion to the severity of the defoliation treatment (Parker and Sampson, 1931; Biswell and Weaver, 1933; De Peralta, 1935; Gernert, 1936; Weaver and Albertson, 1943; Carter and Law, 1948). In some instances the specific gravity also decreased, but this was by no means a consistent trend.

Root Distribution

Defoliation has been noted to retard the growth in length of roots (Parker and Sampson, 1931) (Table 41) so that it is not surprising that certain workers have reported that the maximum depth of penetration of the roots of defoliated plants was less than that of non-defoliated plants (Fitts, 1925; De Peralta, 1935; Hanson and Stoddart, 1940; Hase, 1941; Weaver, 1950).

Klapp (1943) found that defoliation reduced the weight of roots in the lower soil layers to a greater extent than in the upper layers, so that the more severe the defoliation treatment the greater was the concentration of roots in the upper layers of the soil (Table 46). The concentration of roots with increasing severity of defoliation mainly took place in the 0–5 cm. layer at the expense of the 5–10 and 10–15 cm. layers, the maximum depth investigated being 50 cm. A similar trend was noted by Frankena and Goedewaagen (1942) in an experiment with large cores of undisturbed turf and soil taken from a clayey grass field (pp. 79–80). The work of Hanson and Stoddart (1940) comparing grazed and ungrazed swards of *Agropyron inerme* also shows this result. In their investigation the grazed sward had 95% of its roots in the upper 15 cm. layer, and 3% in the 15–30 cm. layer, and the ungrazed sward 92% and 5%, respectively. The results of an experiment of Sprague, H. B. (1933) comparing plants of *Agrostis* spp. and *Festuca ovina* cut at heights of 0·875 in. and 0·25 in. show that the depth of root penetration and root-weight was highest, and the percentage of roots in the 0–1 in. layer lowest, in the plants cut to a height of 0·875 inch. Working with *Lolium perenne*, Baker, H. K. (1955) noted that the plants subjected to his most severe defoliation treatment tended to have a greater proportion of their root weight in the surface horizon (0–1 in.) than undefoliated plants.

The results of other experiments do not, however, show this trend. Those of Weaver (1950) comparing the effect of grazing intensities upon prairie grasses show a reduction in the depth of maximum root penetration due to heavy grazing, but do not show any changes in the percentage distribution in the upper soil layers (0–0·5 ft., 0·5–1·0 ft.) comparable with the grazing intensity. Likewise Thaine (1954) with *Elymus junceus* did not find any variation in the percentage of roots in the 0–6 in., 6–12 in. and 12–18 in. soil layers due to variations in the clipping treatments. Other experiments have, in fact, shown the opposite trend to that found by Klapp. The results of Torstensson (1938) show that swards of *Festuca*

TABLE 46

Root mass and its vertical distribution beneath a mixed sward in its 4th year of differential treatment (*Klapp*, 1943)

Depth (cm.)	Utilisation: Grazed			Utilisation: Mown			
	Weekly	Every 14 days	Every 21 days	Weekly	5 times per season	4 times per season	3 times per season
	Percentage distribution						
0–5	95·23	93·23	90·93	94·83	84·83	87·93	82·88
5–10	2·52	4·08	5·36	2·96	7·03	6·15	9·06
10–15	0·99	1·62	1·98	0·90	3·94	2·68	3·34
15–20	0·48	0·57	1·01	0·87	1·85	1·26	1·66
20–30	0·54	0·42	0·58	0·31	1·63	1·13	1·56
30–40	0·18	0·05	0·11	0·09	0·53	0·57	0·83
40–50	0·06	0·03	0·03	0·04	0·19	0·28	0·67
	Root weight (grams dry matter per 1000 cm.²)						
0–50	31·029	31·833	39·037	31·240	50·450	77·081	71·608

pratensis, *Poa pratensis* and *Phleum pratense* cut to a height of 7 cm., contained a higher percentage of roots in the 0–5 cm. soil layer and a lower percentage in the 20–25 cm. layer than swards cut to a height of 3 cm. In an experiment of H. B. Sprague's (1933), uncut plants of *Poa pratensis* and *Agrostis alba* had a higher percentage of their roots in the 0–1 in. layer than had defoliated plants. Kennedy and Russell (1948) found that the weight of roots plus rhizomes of *Poa pratensis* in the 0–1 in. layer was reduced by defoliation to a greater extent than the weight of roots in the 1–2 in. and 2–3 in. layers. The greater decrease in the 0–1 in. layer may be due to the roots and rhizomes being weighed together, as the rhizomes of *Poa pratensis* have been reported to be more susceptible to the effects of defoliation than the roots (Brown E. M., 1943). This may also have been the case in other experiments.

Both De Peralta (1935) working with *Holcus sorghum sudanensis*, and Hase (1941) working with *Buchloë dactyloides*, *Bouteloua gracilis*, and *B. curtipendula* have noted that the lateral spread of the roots of seedlings was decreased by partial defoliation; but Hanson and Stoddart (1940) found that the lateral spread of grazed plants of *Agropyron inerme* was greater than that of ungrazed plants. This latter observation would need to be repeated under more strictly controlled conditions before it could be regarded as conclusive.

Rhizomes

Defoliation has a similar effect upon rhizomes to that which it has upon roots, but certain investigators have suggested that rhizomes are more severely affected than roots. Graber and Ream (1931) working with *Poa pratensis* found that the formation of new rhizomes was more severely affected by intensive defoliation than was the production of new roots. Young plants of *Agropyron repens* were noted by Dexter (1936) not to produce rhizomes when subjected to severe defoliation treatments.

Cutting swards of *Poa pratensis* twice-monthly to a height of 1 or 2·5 inches was found by Brown, E. M. (1943) to have little or no influence on root development in the upper 6-inch layer of the soil but materially to affect the quantity of rhizomes by retarding their development during the spring and by increasing the rate at which they lost weight during the summer. In the autumn, however, the largest increase in rhizome weight occurred in the plots subjected to the most severe defoliation (1 inch), provided that the moisture supply was adequate for growth at this period.

Several investigators have reported that the weight of the rhizomes at the end of the experimental period decreased with increasing severity of the defoliation treatments. In most experiments, the weight of rhizomes decreased roughly in the same proportion as the weight of roots (Harrison, 1931; Harrison and Hodgson, 1939; Johnson and Dexter, 1939). Other experimenters have simply stated that the weight of roots plus rhizomes decreased (Klapp, 1942; Kennedy and Russell, 1948).

Sturkie (1930) working with *Sorghum halepense* found, as would be expected, that cutting during the latter half of the season did not reduce the rhizome weight to such an extent as did cutting throughout the entire season. But the shoot growth in the following season was reduced equally by both treatments, suggesting that the food reserves were reduced by cutting during the latter half of the season to a greater extent than the weight of the rhizome indicated.

Shoot Growth

The total quantity of shoot growth produced by a plant which is defoliated once or more during a period suitable for growth is normally lower than the quantity produced by a similar plant not defoliated, i.e. original growth plus recovery growth is smaller than uninterrupted growth. The difference varies directly with the intensity of defoliation. Root development, measured at the end of the period, is also reduced in direct proportion to the intensity of defoliation, but to a greater degree than the shoot growth. Thus the weight of root at the end of the experiment expressed as a percentage of the total weight of shoot produced during the experiment plus the weight of roots decreases with the intensity of the defoliation treatment. This applies either to short-term or long-term experiments. Results of this nature were quoted by Graber, Nelson, Leukel and Albert (1927); Sturkie (1930); Stapledon and Milton (1930); Graber (1931); Graber and Ream (1931); Biswell and Weaver (1933); Robertson (1933); De Peralta (1935); Gernert (1936); Roberts and Hunt (1936); Torstensson (1938);

Harrison and Hodgson (1939); Johnson and Dexter (1939); Klapp (1942); Weinmann (1943); Lovvorn (1944); Crider (1945); Carter and Law (1948); Kennedy and Russell (1948); Thaine and Heinrichs (1951); Jacques and Edmond (1952); Albertson, Riegel and Launchbaugh (1953); Thaine (1954) (see Table 53).

The number of tillers produced by a plant and the weight of roots per tiller have been stated by several workers to decrease with defoliation; the greater the severity of the defoliation treatment the greater the decrease in tiller number and weight of root per tiller. (Stapledon, 1924; Stapledon and Milton, 1930; Jacques, 1937a). Jacques (1937a) also found that the number of roots per tiller varied inversely with the severity of the defoliation, a relationship which he expected, since, in his experiment, new roots developed mainly on new tillers.

Baker, H. K. (1955) working with *Lolium perenne* reported that herbage growth in the spring varied with the intensity of the defoliation treatment to which the plants had been subjected the previous autumn. Those plants most leniently defoliated had a high weight of roots per plant and per tiller and produced most herbage growth in the spring.

Species

The severity of the effect of partial defoliation upon a plant would appear to depend upon:—

1. The proportion and the parts (i.e. leaves, stems, stubble or flowers) of the shoot growth removed.
2. The frequency of the defoliation treatment.
3. The quantity of reserve foods held by the plant, which would be expected to vary with the previous environmental conditions and the plant's physiological growth-stage.
4. The hereditary factors which govern the plant's growth-rate.
5. The environment after defoliation, i.e. its suitability for growth.

Factors 3 and 4 will vary with the species; Factor 1 under most experimental conditions will also depend upon the species, since plants are usually cut to a definite height rather than cut so that a known proportion of the shoot is removed; thus a prostrate plant retains a larger proportion of its photosynthetic tissue than does an erect plant.

TABLE 47

Order of resistance to partial defoliation

(*Klapp*, 1937a)

Least resistant	*Phalaris arundinacea*
	Avena elatior
	Bromus inermis
	Avena flavescens
	Alopecurus pratensis
	Dactylis glomerata
	Festuca pratensis
	Poa trivialis
	Agrostis sp.
	Festuca rubra
	Poa pratensis
Most resistant	*Lolium perenne*

Klapp has put forward several ideas concerning the relative susceptibility of species to defoliation. In one paper (1937a) he listed twelve species in order of their relative sensitivity to partial defoliation (Table 47). In the same paper he pointed out that the species which he found to be particularly susceptible to grazing were, according to Witte (1929) (Table 22), deep-rooting, while those which were resistant were shallow-rooting.

In *Poa pratensis*, a species resistant to defoliation, Klapp (1937b) found that the leaf bases (tillering zone) plus roots (i.e. the non-green parts) formed a large proportion of the whole plant while this was less so in the case of *Dactylis glomerata*, a moderately resistant species. In the same paper, Klapp described the following types of grasses:—

i. The extreme type, e.g. *Molinia caerulea*, which cannot bear mowing, even to the extent of two cuts annually. Klapp believed that this species did not begin to store food reserves until late in the autumn and therefore cutting during the growing season seriously weakened the plant because of its lack of reserves.

ii. Species which can thrive even with two, three or four cuts annually, e.g. *Avena elatior*, *Phalaris arundinacea*. These species (according to Klapp) utilised their reserves to a large extent during periods of vigorous growth. They suffered considerably if cut during the early stages of recovery and were characterised by preponderantly tall, erect shoots, slight formation, or absence, of basal leaves and by undergoing a complete rest in winter. Mowing or grazing almost completely removed all their photosynthetic tissue.

TABLE 48

Weight of plant organs after being subjected to defoliation treatments. Figures in relation to those of *Dactylis glomerata*

(*Klapp*, 1942)

Treatment:—	Leaves and haulms			Stubble			Roots and rhizomes		
Species	Average (1)	Most favourable cutting sequence (2)	Most injurious cutting sequence (3)	Average (4)	Most favourable cutting sequence (5)	Most injurious cutting sequence (6)	Average (7)	Most favourable cutting sequence (8)	Most injurious cutting sequence (9)
Festuca rubra	91	90	84	94	33	185	197	105	320
Poa pratensis	89	79	88	73	41	97	191	182	178
Dactylis glomerata	100	100	100	100	100	100	100	100	100
Lolium perenne	107	112	110	66	44	94	106	97	112
Bromus inermis	100	107	98	74	36	50	108	132	129
Phleum pratense	167	174	165	101	88	109	52	47	50
Phalaris arundinacea	133	140	111	44	40	37	231	220	200
Festuca pratensis	89	113	60	49	40	55	74	88	61
Avena elatior	114	139	92	59	61	53	72	99	57
Poa palustris	60	99	39	40	44	46	45	49	67
Triticum caninum	80	126	42	27	37	15	17	22	10

iii. Species which in a sward are neither encouraged not discouraged by frequent mowing or grazing, e.g. *Dactylis glomerata*, *Festuca pratensis*. These exhibited a preponderance of basal leaves.

iv. The pasture type, e.g. *Lolium perenne*, *Poa pratensis*. These were prostrate plants so that it was difficult to remove all their photosynthetic tissue by cutting or grazing. They were often characterized by a long growth period during winter.

The results of several experiments were summarised by Klapp in a later paper (1942) (Table 48). On the whole those species whose shoot growth was not greatly affected by variations in the severity of the defoliation treatments, i.e. were resistant to defoliation (those species exhibiting little decrease or even an increase from column 2 to 3 in Table 48), were distinguished by a large bulk of root and rhizome and a relative increase of root and stubble bulk when the most favourable cutting treatment was compared with the most injurious (columns 5 and 6, and 8 and 9 of Table 48). The species tested were divided by Klapp into the following groups:

a. Those species with stubble especially capable of rapid assimilation, having most rapid aftergrowth and a good endowment of roots, e.g. *Dactylis glomerata*, *Phleum pratense*, and *Lolium perenne*.

b. Rhizome-producing grasses with a particularly high proportion of root and rhizome and an abundant bulk of stubble: a relative increase or, at least, no decrease of the stubble and rhizome portion relative to *Dactylis glomerata* (Table 48) under frequent cutting, e.g. *Festuca rubra*, *Poa pratensis*.

c. Grasses with stubble poor in leaves and small in bulk, both absolutely and relatively (Table 48), decreasing under frequent cutting (*Avena elatior* and *Phalaris arundinacea*), and in which the great mass of rhizomes capable of storage cannot compensate for the ineffective stubble. Relative diminution of the subterranean organs under frequent cutting (Table 48).

d. Grasses with absolutely and relatively small bulk of stubble and roots resulting in the death of a large number of plants when subjected to frequent cutting, e.g. *Poa palustris*, *Triticum caninum*.

In groups (a) and (b) are found the species relatively resistant to cutting, and in (c) and (d) those relatively susceptible. The two classifications (1937b and 1942) of Klapp resemble each other in several respects.

No other worker appears to have been primarily interested in the relative resistance of species to defoliation. The results that are available are the by-product of experiments designed to study other variables (Biswell and Weaver, 1933; Roberts and Hunt, 1936; Jacques, 1937a; Harrison

and Hodgson, 1939; Carter and Law, 1948). No general conclusion is evident, and, in view of the nature of the experiments, other conclusions would not appear to be warranted.

Unusual Results

Certain investigators have reported results which are not in complete agreement with those previously discussed. Weinmann and Goldsmith (1948) working with *Cynodon dactylon* found in one experiment that clipping treatments had no effect upon the root- and rhizome-weight; in another experiment those plants receiving an NPK fertilizer were likewise unaffected but those not receiving the fertilizer had their weight of rhizomes, but not roots, decreased by clipping. In a further experiment the plants were completely defoliated by means of scissors and the weight of roots and rhizomes was soon lowered. *Cynodon dactylon* is an extremely prostrate grass with numerous large rhizomes. The clipping treatments could not have removed sufficient photosynthetic tissue to produce a measurable effect. Similarly Ruby and Young (1953) found that clipping treatments did not affect the root weight of *Paspalum plicatulum*, a species which produces a leafy basal growth.

In *Poa pratensis*, another species resistant to clipping on account of its prostrate habit of growth, Brown, E. M. (1943) noted that the root weights did not differ much between several clipping treatments, but the rhizome weights were affected according to the severity of the treatment (p. 99).

Working with *Lolium perenne*, Baker, H. K. (1955) found that the weight of root per plant of both spaced plants and plants in a sward decreased with increasing intensity of defoliation treatment, but that the root weight per unit area of sward did not. This was because the plant density in the sward was increased by defoliation. A similar explanation may be used to account for the result of Stevenson and White (1941) in Canada, who reported that grazed prairie yielded a larger root weight than ungrazed prairie.

In all the experiments discussed in this chapter, the shoot growth removed was for the most part functional and capable of photosynthesis. If the shoot tissue had been dead, then it is possible that results showing increased growth due to defoliation would have been obtained, since the removal of dead tissue might have, possibly, allowed the active photosynthetic tissue remaining to function more effectively and so enabled the plant to replace the dead tissue by active tissue.

CHAPTER 20

ROOT PRUNING

The pruning of a plant's roots results in an increase in the rate of root initiation, and, if the severed root is long enough and young enough it also results in an increase in the number of laterals produced on the remaining portion of the pruned root: the growth rate of the shoot is also reduced.

Most of the roots of established plants of *Lolium* spp. and *Dactylis glomerata* were reported by Jacques (1944) to react to pruning by the production of laterals, but roots less than one inch in length between the proximal end and place of severance rarely showed this regenerative power unless they had recently been initiated. As the roots became older they progressively lost their power to produce laterals. *Dactylis glomerata* and *Lolium perenne* reacted most vigorously to severance; *Lolium multiflorum* and *Lolium westerwoldicum* least.

In further work, Jacques and Edmond (1952) studied the effect of root amputation on shoot and root growth as a whole. A number of established plants had all roots except six amputated, and, thereafter, all new roots cut off at weekly intervals, the number of roots cut off being recorded. An equal number of plants was not subjected to this treatment, their roots being counted at the termination of the experiment. Superimposed upon this comparison were six defoliation treatments, the herbage being cut at a height of 0·5, 1 or 2 inches at weekly or fortnightly intervals. The experiment lasted forty weeks. At the end of this period it was found that root amputation had increased the number of roots initiated, the number that were produced and cut off increasing with the leniency of defoliation (Table 49). The investigators commented upon this stating that the more severe the defoliation treatment the greater was the tendency for the formation of leaf before root, the prior demand of the plant being for photosynthetic tissue, and, until such time as this was formed, an increase in the absorptive area of the roots was of little importance. *Dactylis glomerata* initiated comparatively few new roots in response to amputation, while 'certified' *Lolium perenne* initiated a relatively large number, 'uncertified' *Lolium perenne* being intermediate.

Root amputation decreased the total sum of herbage produced during the course of the experiment, the more lenient the defoliation treatment the greater being the proportionate reduction. An 'initial' stimulus was, however, given to herbage production by amputation, the

TABLE 49

Number of roots initiated
(Treatment mean numbers)
(*Jacques and Edmond*, 1952)

Height of cutting	Root treatment	Frequency of cutting	*Lolium perenne* (certified)	*Lolium perenne* (uncertified)	*Dactylis glomerata*
0·5 in.	Weekly pruning	Weekly	355	235	222
	,, ,,	Fortnightly	454	367	327
	Terminal pruning	Weekly	114	133	154
	,, ,,	Fortnightly	185	212	244
1 in.	Weekly pruning	Weekly	418	308	265
	,, ,,	Fortnightly	616	478	355
	Terminal pruning	Weekly	146	201	197
	,, ,,	Fortnightly	239	246	338
2 in.	Weekly pruning	Weekly	769	567	441
	,, ,,	Fortnightly	903	703	524
	Terminal pruning	Weekly	241	280	303
	,, ,,	Fortnightly	394	356	414

General Mean = 353 General Mean of weekly pruning = 461

plants so treated out-yielding those with complete root systems during the first few weeks of the experiment, the position being reversed for the remainder of the time. The period of this initial stimulus lengthened with the severity of the defoliation treatment.

Working with seedlings of *Holcus sorghum sudanensis*, Nedrow (1937) concluded that the cutting of all roots at a depth of 5 or 10 inches greatly reduced the growth of both the roots and the shoots of the plants so treated, the reduction tending to increase with successive treatments. Other, similar experiments are discussed on p. 75.

Graber (1929), and Graber, Fluke and Dexter (1931) have studied the damage done to pastures in Wisconsin by 'white grubs' (the larvae of *Phyllophaga* spp.) eating through the roots and rhizomes of *Poa pratensis* in such a manner as to sever the contact of large areas of sod with their root system. The injury was largely prevalent where the root and rhizome growth had been limited by close grazing or low fertility. The life history of this group of insects and the damage they do has been discussed by Hammond (1948) and by Dumbleton (1942).

CHAPTER 21

MINERAL NUTRITION

The rate of uptake of an ion from the soil by a plant's roots varies with the species, the plant's age, the ion concerned and the environmental conditions. Certain workers, e.g. Drake, Vengris and Colby (1951), McLean and Baker (1953), McLean and Adams (1954), have attempted to explain these variations, at least in part, as being due to variations in the cation exchange capacities of the roots and the valency of the ions. The rate of uptake of molecules of P^{32}, by strains of *Cynodon dactylon* and *Paspalum notatum* has been studied by Burton, De Vane and Carter (1954). This rate varied with each strain and could not be related to the strain's weight of roots. But it decreased rapidly with depth, as did the weight of roots; also the rate of decrease was least in those strains with a high percentage of their root-weight in the lower layers of the soil. It is possible that between plants within a strain the rate of uptake varies with the weight of roots.

Once an ion has been absorbed by a plant the use to which it is put by the plant, and therefore its 'effect' upon the plant will depend upon the balance between the elements which the plant is absorbing at that particular time, the environment, and the plant's 'need' at that time for the particular elements contained in that ion. Each element may be considered as a separate 'growth factor' but the mineral elements seem to be more closely related to each other than are the other factors.

Nitrogenous Nutrition

The action of the nitrogenous constituents in the growth media is not yet fully understood. The investigations into this subject have been carried out under a diversity of conditions, which no doubt accounts for some of the apparent discrepancies in the results, summarised in this chapter. Also nitrogen is usually supplied in fertilizers either as ammonium- or nitrate-ions and under certain conditions these two forms of nitrogen may have different effects upon the plant. In addition to obtaining nitrogen by absorption from the growth medium it is also possible in certain circumstances that the plant receives nitrogen from mycorrhiza (p. 12) or symbiotic bacteria (Notlev, 1938) in its roots.

In general, it appears that plants grown in conditions where available nitrogen was a factor limiting growth have a well developed root system, but a poorly developed shoot system. Plants grown with an excess of nitrogen exhibit the opposite relative development. The addition of available nitrogen to the nutrient media of plants, which previously had no excess nitrogen, results in an increased growth of both shoot and root and a decrease in the percentage of the plant's weight in the roots, i.e. shoot growth is accelerated to a greater extent than root growth. Further increases produce smaller and smaller increases in root growth until a point is reached where further increases cause a retardation of growth. Thus, the effect of a moderate increase in the nitrogen supply is to increase a plant's root weight compared with that of a plant receiving a lesser supply, but further increases result in the plant having a lower root weight than one receiving a less liberal supply of nitrogen. The nitrogen supply has a similar effect upon the shoot growth in that the response to a unit quantity of nitrogen becomes smaller and smaller but no adverse effects, i.e. retardation in growth due to excess nitrogen, were noted with the concentrations of nitrogen used in the experiments discussed here. If factors other than nitrogen supply limit growth, then the effects of a nitrogen supply in excess of normal requirements are mitigated.

The action of additional nitrogen has been explained by Sprague, H. B. (1934) on the basis that a narrow ratio of soluble nitrogen to carbohydrate reserves in the plant favours shoot development rather than root development. Watkins (1940) stated that under normal conditions there is a tendency to excess carbohydrate storage in the underground parts and that this condition may be altered by stimulating the top growth with extra available nitrogen. The situation for all plants has been summarised by Steele (1949) who stated that the amount of nitrogen absorbed by a plant alters the carbon/nitrogen ratio in its tissues. A narrow ratio leads to vigorous vegetative growth while a wide ratio leads to good development of the reproductive tissues.

The general effect of increasing the available nitrogen supply is illustrated by two experiments

TABLE 50

Weight (grams dry weight) of root plus stubble and of shoot of *Agrostis tenuis* plants grown in sand culture as affected by nutrient solutions

(*Sprague, H. B.*, 1934)

Nutrient solutions	Weight of root plus stubble	Weight of shoot	Percentage of the plant's weight in the roots plus stubble
Standard	3·20	4·65	41
„ plus light rate ammonium sulphate	2·70	4·05	40
„ „ heavy „ „ „	2·60	3·45	43
„ „ light „ sodium nitrate	4·95	7·55	40
„ „ heavy „ „ „	5·30	8·25	39
„ „ light „ ammonium chloride	2·85	3·90	42
„ „ heavy „ „ „	2·75	2·90	49
„ „ light „ sodium chloride	3·15	3·45	48
„ „ heavy „ „ „	3·15	3·15	50
„ „ heavy „ sodium sulphate	3·40	5·10	40

of H. B. Sprague's (1934). One series of plants of *Agrostis tenuis* was grown in sand culture with a standard nutrient solution containing adequate nitrogen, while another series was grown with a solution containing additional nitrogen in the form of sodium nitrate. In one experiment, which was conducted during the winter months, the additional sodium nitrate resulted in an increase in the root weight and a slight decrease in the percentage of the plant's weight in the root (Table 50). In another experiment, which was conducted during the spring, i.e. with better external conditions for growth, the root weight was decreased by the additional nitrogen as was the percentage of the plant's weight in the roots while the weight of the plant as a whole increased (Table 51). A similar result was obtained by Harrison (1934) in spring with *Poa pratensis*.

An experiment was carried out by Benedict and Brown (1944) in which plants of *Agropyron smithii* and *Bouteloua gracilis* growing in sand culture were deprived of both nitrate- and ammonium-nitrogen for a time. At the end of this period these plants had smaller root weights and a larger percentage of their weight in the roots than had plants which had received nitrogen during the whole period. After a further period during which all plants received nitrogen, those which had always received nitrogen still had larger root weights and a lower percentage of their weight in

TABLE 51

Weight (grams dry weight) of root plus stubble and of shoot of *Agrostis tenuis* plants grown in sand culture as affected by nutrient solutions

(*Sprague, H. B.*, 1934)

Nutrient solutions	Weight of root plus stubble	Weight of shoot	Percentage of the plant's weight in the roots
Solutions with reactions approximately pH 4·5			
Standard	13·0	18·6	41
„ plus light rate ammonium sulphate	10·0	11·6	46
„ „ heavy „ „ „	7·0	10·0	41
„ „ light „ sodium nitrate	11·7	26·0	31
„ „ heavy „ „ „	10·6	26·9	28
Average	10·6	18·7	37
Solutions with reactions approximately pH 6·5			
Standard	11·4	22·2	34
„ plus light rate ammonium sulphate	9·9	22·5	31
„ „ heavy „ „ „	7·8	19·6	29
„ „ light „ sodium nitrate	7·4	25·9	22
„ „ heavy „ „ „	7·0	25·2	22
Average	8·7	23·1	27

the roots. The plants of *Bouteloua gracilis* which had been without nitrogen for a time showed a decrease in the percentage of their weight in the roots when nitrogen became available, but this was not always the case with *Agropyron smithii*.

The addition of a nitrogenous fertilizer containing both nitrate- and ammonium-ions was found by Troughton (1956) to increase both the root and shoot growth of young undefoliated plants of *Lolium perenne* and *Phleum pratense*; the growth rate of the shoot system was increased relative to that of the roots, and this was reflected in a decrease in the percentage of the plant's weight in the roots.

Reid (1933a) working with *Agrostis palustris* in sand culture found that the total weight of herbage production increased with the amount of nitrogenous fertilizer applied while the root weight correspondingly decreased. With a small supply of nitrogen a relatively large and deep root system was produced, while with an extremely large supply of nitrogen and a normally adequate supply of other essential elements there was a weak development of the root system, and the roots, which were short, tended to be coarse, not profusely branched and of a reddish-brown colour. When grown in water culture, plants of *Phleum pratense* were found by Knoblauch, Ahlgren and Gausman (1955) to produce short, heavy-textured and succulent root systems when the level of nitrogen in the substrate was high and medium (315 and 126 ppm., respectively); when the level of nitrogen was low (21 ppm.) an extensive, fine-textured, fibrous root system was produced. Similar differences occurred in the field.

Under field conditions in the Netherlands, Goedewaagen (1952) found that the application of a nitrogenous fertilizer to a sward on a sandy soil increased the yield of hay but decreased the weight of roots compared with plots not receiving a nitrogenous fertilizer. The decrease in root weight was more pronounced in the lower layers of the soil than in the upper layers.

Nitrate- and Ammonium-Ions

Nitrogen is commonly supplied to plants in fertilizers either in the form of nitrate- or ammonium-ions; of these, nitrate is considered to be the most easily assimilated. Darrow (1939) compared the effects of nitrogen supplied in these forms to *Poa pratensis* growing in sand culture, in an experiment where pH and temperature were also variables. The plants received no nitrogen except in the form of either one or other of these ions. The plants supplied with nitrate nitrogen showed markedly better development than did those supplied with ammonium nitrogen, producing greater dry weights of roots, shoots and rhizomes (Table 52). The extent of the root system was the same in both cases, but a more rapid elongation of the root tips of the nitrate-ion plants took place at 59 and 77°F. but not at 95°F., when the ammonium-ion plants excelled slightly.

TABLE 52

Weight of roots and shoot of plants of *Poa pratensis* as affected by temperature, nitrogen ion and pH of the growth medium. Weights in grams per plant

(*Darrow*, 1939)

	Root weight		Shoot weight		Percentage of the plant's weight in the roots	
Nitrogen Ion:—	Nitrate	Ammonium	Nitrate	Ammonium	Nitrate	Ammonium
Temperature and pH						
59°F.						
pH 4·5	4·06	0·85	3·40	0·26	54	77
5·5	3·96	1·07	3·48	0·58	53	65
6·5	4·50	2·65	3·59	1·71	56	61
77°F.						
pH 4·5	5·62	0·91	2·58	0·24	68	79
5·5	4·25	1·10	3·27	0·88	56	56
6·5	4·78	2·00	3·13	1·77	60	53
95°F.						
pH 4·5	3·31	0·44	1·62	0·14	67	76
5·5	2·91	0·65	1·56	0·27	65	70
6·5	2·21	0·87	1·13	0·43	66	67

Root weights of the nitrate-ion plants varied little with differences in the pH, whereas the root and rhizome development was greatest in the ammonium-ion plants at the high pH (6·5). These latter plants had the most extensive development of laterals while at the lower pH there was a predominance of stunted knobbly laterals, especially near the base of the main laterals. The percentage of the plant's weight in the roots produced by the ammonium-ion plants decreased with increasing pH.

In a similar experiment with constant pH (4·5–4·8) and temperature, Harrison (1934) produced larger plants of *Poa pratensis* with nitrate nitrogen than with ammonium nitrogen.

The effect of adding additional nitrogen in the form of ammonium- or nitrate-ions to plants of *Agrostis tenuis* growing in sand and already receiving some nitrogen in culture solution was studied by Sprague, H. B. (1934). The results obtained with the nitrates have already been mentioned (pp. 105–6). During the winter months, with a culture solution of pH 4·6–5·1, the addition of ammonium sulphate or ammonium chloride to the basal nutrient solution resulted in a reduction of both the weight of the roots and shoots, while the addition of nitrates increased the weight of both roots and shoots compared with those plants receiving the basal solution only (Table 50). During the spring, i.e. when conditions were more favourable to growth, with a solution of pH 4·5 the addition of ammonium sulphate still inhibited both the growth of the roots and the shoots. With a solution of pH 6·5 the root growth was inhibited but the shoot growth less so, resulting in a lower percentage of the plant's weight occurring in the roots (Table 51). At both pH levels, the nitrate caused a relative decrease in the root growth and an increase in shoot growth. In other experiments the level of pH at which the ammonium ion ceased to have an adverse effect upon growth varied with the species.

Under field conditions on the South African veld, in an experiment concerned with the interaction of defoliation and nitrogen supply, Weinmann (1943) (Table 54) showed that plots receiving sodium nitrate as a fertilizer had slightly higher root weights than had those receiving ammonium sulphate; most of these differences were not, however, statistically significant. Both series of plots acted in the same manner to the different intensities of defoliation, and showed roughly the same relationship to plots not receiving nitrogenous fertilizer. Evans, T. W. (1931) stated that applications of both ammonium sulphate and sodium nitrate had a deleterious effect upon the root development of *Agrostis* and *Festuca* spp. which were growing in a field sward and were frequently defoliated. The addition of ferrous sulphate counteracted the effect of ammonium sulphate.

The differences in reaction to nitrate- and ammonium-nutrition are probably due to two factors: the ease with which the plants can assimilate the two ions and the toxicity of the ammonium ion. It has long been known that grasses can absorb nitrates from the soil but only recently has evidence been accumulating to suggest that grasses can also absorb ammonium salts (Richardson, H. L., 1938; Steele, 1949). The relative ease of assimilation depends partly upon the age of the plant (ammonium absorption predominating in the younger stages of plant growth and nitrate absorption later) and partly upon the pH of the media, maximum absorption of ammonium ions occurring in a slightly acid medium (Blackman, 1932; Steele, 1949). The experiments of Darrow and Sprague showed that the effect of the ammonium ions on growth more nearly approached that of the nitrate ions in a medium of pH 6·5 than in one with a lower pH, and when conditions were favourable for growth than when they were unfavourable.

The ammonium ion has been shown to be toxic to dicotyledons with a low supply of carbohydrates and/or a low supply of organic acids, but the Gramineae have shown themselves able to withstand high concentrations of this ion (Blackman, 1932). In the dicotyledons, it has been shown that the toxicity is accentuated by the addition of ferrous sulphate to the nutrient media, and Jones and Shive (1921) have shown that the addition of this compound accentuated the toxicity of ammonium ions supplied to wheat plants (*Triticum* sp.) growing in sand culture, except when the ferrous sulphate was supplied in very small quantities in which case it caused the effects of toxicity to disappear. This may explain the observations of Evans that ferrous sulphate counteracted the deleterious effect of ammonium sulphate on swards of *Agrostis* and *Festuca* spp.

The magnitude of the differences between the effects of nitrate- and ammonium-ions has not been fully determined in the field, but it would seem

unlikely to be very great, the ammonium ions apparently acting in the same manner as the nitrate ions, but with less intensity. This is assuming that other factors, e.g. pH, remain constant. Nitrogen applied as either ion in the field has the same effect on the top growth, except that the nitrate ion is usually slightly quicker in acting. The three experimenters (Darrow, Harrison and Sprague), who have critically compared the two ions and have found marked differences between them, used sand cultures. Weinmann and Evans, working in the field, did not find such differences. It is possible that in the soil the micro-organisms or other factors act in such a manner as to mitigate the ill effects of excess ammonium ions.

Applications of ammonium sulphate to swards of *Bromus inermis* were stated by Watkins (1940) to increase the root growth during the plant's early stages of growth but to retard the root growth later. Rhizome growth was decreased and shoot- and stubble-growth increased at all stages of growth. Shade was found to have a deleterious effect upon both the root- and shoot-growth (p. 90). The application of ammonium sulphate to shaded plants caused a further reduction in root weight and increase in shoot weight.

The effect upon the rhizomes of treating plants of *Agropyron repens* with dressings of ammonium sulphate has been described by Dexter (1936). The plants were given dressings of ammonium sulphate, and, after a period of growth, the rhizomes were detached from the rest of the plant and allowed to grow independently. The rhizomes from plants liberally supplied with nitrogen sprouted more freely than did those from plants grown with little nitrogen. The shoots from the rhizomes of the treated plants were larger, heavier, and contained a higher percentage of nitrogen but had a lower percentage of dry-matter than those from plants grown with little nitrogen. The rhizomes from the 'plus' nitrogen plants remaining after sprouting had ceased contained more nitrogen and less dry matter than those from the 'minus' nitrogen plants. Plants receiving phosphorus and potassium in addition to nitrogen stored less nitrogen in their rhizomes than did those receiving nitrogen only. Under conditions of heavy fertilization, no plants were produced which could be considered low in carbohydrates. Storage, as evinced by the formation of rhizomes and the ability of old rhizomes to sprout vigorously, occurred even in the most highly fertilized plants. Dexter was concerned with the eradication of this species and the possible stimulation of shoot growth at the expense of the food reserves; under the conditions of his experiment the quality of the reserves apparently was increased by the application of fertilizer.

Nitrogen Supply and Defoliation

The relationship between these two factors appears to be complex, conflicting results having been reported by different workers. The effect of defoliation, when considered alone, is to reduce the growth of the whole plant, the growth of the roots being affected to a greater degree than that

TABLE 53

Effect of defoliation treatments on *Dactylis glomerata* plants.
Weight of total production of shoots, weight of roots and number of tillers at the end of the investigation and weight of roots expressed as a percentage of the total shoot plus root weight.
Weights and numbers per plant

(*Stapledon and Milton*, 1930)

		With nitrogen fertilizer				Without nitrogen fertilizer			
Treatment	Number of herbage cuts	Weight of Shoots	Weight of Roots	Weight of roots as a percentage of total weight	Number of tillers	Weight of Shoots	Weight of Roots	Weight of roots as a percentage of total weight	Number of tillers
Cut to ground-level	10	78·9	1·8	2	152	52·5	2·1	4	138
Cut to 6 in.	8	106·4	6·9	6	230	72·0	5·8	7	204
Hay and aftermath cuts	2	212·0	10·9	5	230	115·0	6·6	5	165
Inflorescences plucked	1	133·0	16·0	11	297	82·0	10·6	11	269

of the shoots. Additional available nitrogen increases the growth of undefoliated plants, especially of the shoots. Thus it may be expected that these two factors may counterbalance each other with regard to total growth but not with regard to the distribution of this growth. The situation does not, however, appear to be as simple as this. In the experiments reported in the literature, defoliation had a greater effect upon the roots than had nitrogenous manuring. There is considerable difficulty in comparing the several experiments, as the intensities of defoliation and quantities of additional nitrogen, as well as the environments and species, varied greatly between the experimenters.

In an experiment reported by Stapledon and Milton (1930) (Table 53), a nitrogen fertilizer produced an increased growth of both root and shoot by plants of *Dactylis glomerata* growing in soil when the plants were subjected to three intensities of defoliation. But when they were subjected to a severer defoliation treatment the nitrogen decreased the root weight very slightly. The same trends were found in the weight of root per tiller. Highveld in South Africa, which had as its predominant species *Trachypogon plumosus*, as indicated by the results of Weinmann (1943) (Table 54), responded to additional nitrogen, either as ammonium sulphate or sodium nitrate, by increased shoot growth and, to a lesser extent, root growth, when the plants were clipped once, twice, or four times per year. When the plants were clipped eight times per year, the additional nitrogen produced a statistically significant increase in herbage growth during the first year of treatment but not in the second; the weight of roots was very slightly lower than that of the control plot, but this reduction was not statistically significant. Plants of *Agropyron repens* growing in sand culture were found by Johnson and Dexter (1939) to respond to additional nitrogen by increased shoot growth and decreased root growth under all their defoliation treatments; the weight of rhizomes also decreased except under the lenient defoliation treatment. The additional nitrogen considerably increased both the rhizome- and shoot-weight of plants which were not defoliated, while the root weight was decreased very slightly.

On the basis of these experiments it would appear possible to state that additional nitrogen increased root- or root-plus-rhizome-weight under conditions of lenient defoliation, and decreased or had no effect on it under conditions of severe defoliation. But the variations in root weight due to the nitrogen treatments were very small and too much reliance cannot be placed upon them. Also this conclusion is not borne out by other experiments. Applications of ammonium sulphate, according to the results of Harrison (1931), decreased the weight of roots under swards of *Poa pratensis* and *Festuca rubra* growing in boxes, when defoliated to heights of 3 inches, but increased the weight under swards defoliated to a height of 0·5 inch. There was considerable variation between the replicates in this experiment, so that while too much reliance cannot be placed on the results, they certainly do not show the trends of the previous experiments. The effect on the rhizomes of *Poa pratensis* was not stated. The results of Graber and Ream (1931) also do not show these trends. The root weight of plants of *Poa pratensis* growing in a mixture of half soil and half sand was not materially influenced by applications of ammonium sulphate under any system of defoliation. Total shoot growth was only increased under the most lenient defoliation treatment. The weight of 'old' rhizomes was decreased by the application of fertilizer and that of 'new' rhizomes increased; no consistent variation with defoliation treatment was observed.

Other experiments have also been reported in which nitrogenous fertilizers decreased the weight of roots of plants subjected to defoliation. This was found by Harrison (1931) with swards of *Poa pratensis*, *Festuca rubra*, and *Agrostis capillaris* cut to a height of 0·25 inch which received applications of ammonium sulphate. In an experiment with *Poa pratensis* growing in sand culture and being severely defoliated, the same result was obtained with calcium nitrate (Harrison, 1934).

Under conditions of very frequent defoliation in the field, Evans, T. W. (1931) found that dressings of ammonium sulphate and sodium nitrate had a deleterious effect on the root systems of swards of *Agrostis tenuis*, *Festuca rubra*, and *Festuca ovina*, while a dressing of ammonium phosphate had a beneficial effect. The deleterious effect of ammonium sulphate was counteracted by a dressing of ferrous sulphate.

In most experiments the shoot growth was increased by the additional nitrogen, the increase being greatest under the lenient defoliation treatments. Several workers have reported that under a severe system of defoliation the additional

nitrogen increased the shoot growth only for a short time after its application (Stapledon and Beddows, 1926; Harrison, 1934; Weinmann, 1943).

The length of time the influence of a dressing of nitrogenous fertilizer lasts will depend upon many factors. Stapledon and Beddows (1926) in Wales found that one year after an application of sodium nitrate there was little indication of its influence on plants of *Dactylis glomerata*, regardless of whether they had been defoliated once or six times during this period.

Under a system of thrice-weekly defoliation, Bell and De France (1944) stated that applications of a fertilizer containing nitrate-, ammonium- and organic-nitrogen caused an increase in the root weight of swards of two species of *Agrostis* after several years of application. Another species of *Agrostis* was stated to have become 'root-bound', so that increasing amounts of fertilizer failed to change the root weight. The root weight was measured in this experiment after a period of years, so that it was actually the balance between growth and decay which was being measured, not growth alone. The pH of the soil was decreased by the fertilizer and this would probably affect the rate of decay. This experiment cannot be stated to reflect the effect of the fertilizer on root growth.

Nitrogen Supply and Temperature

This interaction was the subject of an experiment by Harrison (1934) with *Poa pratensis*, the nitrogen being supplied in nitrate form. His results may be summarised as follows:

1. At 60°F. without nitrogen. No rhizomes were pushed out of the soil. Many new roots were formed.
2. At 60°F. plus nitrates. Many rhizomes, which were below ground at the beginning of the experiment, turned upwards and pushed above ground. No new roots were produced.
3. At 80°F. without nitrogen. Some rhizomes gradually appeared above ground. No new roots were produced.
4. At 80°F. plus nitrates. No rhizomes appeared above ground. No new roots were produced; many roots and rhizomes died.
5. At 100°F. with and without nitrates. Rhizome tips and roots practically all died.

The plants were defoliated frequently during the experiment. Additional nitrate appears to have accentuated the effects of temperature. Harrison explained these results as being due to the nitrogen fertilizer stimulating the shoot growth after defoliation, and consequently causing a larger drain upon the carbohydrate reserves in the roots and rhizomes. In the late autumn and winter, a lack of nitrogen resulted in the rhizomes failing to emerge above the soil level; a long photoperiod had the same effect (see also the work of Darrow, 1939) (pp. 107–8).

Time of Application of Nitrogenous Fertilizers

The effect of several applications of sodium nitrate at short intervals of time to plants of *Dactylis glomerata* was found by Stapledon and Milton (1930) to be cumulative, the increase in root weight over control plants not being as consistent early in the experiment when only a small quantity of nitrate had been applied as it was later, when a greater quantity had been applied. Working in Russia, Bronzova (1940) stated that the fractional application of nitrogenous fertilizer was most effective in increasing the root weight under a system of cutting for hay and aftermath, when applied in the initial period of growth and after the first cut. With a single application, the best time was during the tillering period. Evidently Bronzova did not apply excess. Sprague, H. B. (1933) considered that slowly available nitrogenous fertilizers permitted greater root development than did soluble fertilizers supplying the same amount of nitrogen.

Phosphatic Nutrition

It was the opinion of several of the older workers that the phosphatic component of the nutrient media had some specific beneficial effect upon the roots of plants. This hypothesis is now largely discredited but the exact function of this element is still not known.

Reid (1933a) reported an experiment in which plants of *Agrostis palustris* were grown in sand culture for three months with three levels of phosphorus supply. The plants receiving a high level of phosphorus nutrition had longer, finer and more branched roots than the plants receiving a low level of phosphorus nutrition. The roots of the latter were much coarser than the former. The weight of the shoots and roots increased with

increasing phosphorus supply; the distribution of the plant's weight between root and shoot systems showed no consistent variations. In New Zealand the weight of root and shoot produced by plants of *Lolium perenne*, *Dactylis glomerata* and *Trifolium repens* were increased during four seasons' growth by the application of superphosphate to the seed-bed when the plants were grown in containers. The percentage of the plant's weight in the roots decreased. Under sward conditions in the field, no consistent effect on root weight was observed (Jacques 1943). In a field experiment on sandy soil in the Netherlands the application of a phosphatic fertilizer increased root weight and the yield of hay very slightly (Goedewaagen, 1952). After several years of application, phosphatic fertilizers were found not to have influenced the weight of roots under a sward of *Cynodon dactylon* (Hall, Meredith, Murray and Altona, 1948).

The results of Stapledon and Beddows (1926) indicated that fertilizing *Dactylis glomerata* with superphosphate under a system of cutting twice a year decreased the weight of both the roots and herbage, while under a system of six cuts per year the herbage weight alone was decreased. Under a system of severe defoliation, Bell and De France (1944) found that the weights of roots, which had accumulated under swards of three *Agrostis* spp. after some years of fertilizing, decreased with the increasing percentage of phosphorus in the fertilizer. The soil pH was little affected by the fertilizers.

Increasing the supply of phosphorus to plants has therefore been reported (1) to increase, (2) to decrease and (3) not to affect, the weight of root and shoot. It seems unlikely from the conditions of the experiments that any of the plants without the additional phosphorus suffered from a severe deficiency, except in the case of Reid's low-level plants. Nor is it likely that a large excess was given to cause any damage. The results of Stapledon and Beddows and those of Bell and De France might be taken to suggest that an interaction between defoliation intensity and phosphorus level exists, but this is not borne out by Reid's experiments in which the results were obtained with plants 'cut to form a turf' and with plants left uncut. Species differentiation is not obvious. Further experiments are required before the action of this element can be clearly stated.

The application of ammonium phosphate compared with ammonium sulphate to plants growing in boxes with soil was found by Harrison (1931) to result in smaller root growth by *Festuca rubra* and *Poa pratensis*. Working under field conditions with swards of *Agrostis* spp., applications of ammonium phosphate were found by Evans, T. W. (1931) to produce a greater root system than ammonium sulphate, whilst Sprague, H. B. (1933) reported the opposite result. Harrison examined his plants 3 months after the first fertilizer application, Evans after 18 months and Sprague after 5 years. The soil pH of Sprague's sulphate plots was lower than that of the phosphate plots and this may account for the discrepancy in the results, the lower pH retarding the decomposition of old roots.

In the experiments mentioned previously, Jacques (1943) studied the effect of adding superphosphate to the seed-bed, (1) as a top dressing, (2) incorporated in the top 6 inches of soil and (3) placed as a layer at a depth of 6 inches. In field trials, the superphosphate, especially when applied as a top dressing, resulted in an increased percentage of the root weight being found in the 0–4 in. layer of the soil, compared with the 4–12 in. layer. No distinct effect upon root weight was observed. In an experiment in which the plants were grown in containers, the superphosphate caused an increase in root weight and a decrease in the percentage of the plant's weight in the roots, especially in the plants receiving it as a sub-surface application. Application of superphosphate as a sub-surface dressing led in most cases to the production of large numbers of roots and tillers, tending towards a high number of roots per tiller, whilst a surface dressing increased root numbers without increasing tiller numbers. As the root weight in the soil decreased rapidly with depth, and shortage of moisture on the soil surface could not account for the results, Jacques concluded that 'over the season as a whole the surface roots of grasses (weight for weight) were less effective than the deep-seated ones in procuring food, even where the fertilizer was concentrated in a layer for them, and despite the somewhat better growth in the establishment period'. It would seem that more critical work is required before this hypothesis is fully substantiated, but it may possibly be connected with loss of cortex by the proximal ends of roots (p. 8).

Potassic Nutrition

Reid (1933a) in an experiment similar to those on phosphorus and nitrogen nutrition, grew plants of *Agrostis palustris* in sand culture with three levels of potassium. The weights of both roots and shoots increased with the increasing abundance of potassium. The 'low' potassium plants had stunted roots. In a similar experiment with *Poa pratensis* the number of rhizomes, their length and tendency to branch, all increased with the potassium content of the nutrient solution. A similar result was obtained with nitrogen.

The weight of both roots and hay was greatly increased by the application of a potassic fertilizer to a sward on a sandy soil in Holland (Goedewaagen, 1952). The increase in weight did not affect the relative vertical distribution of the roots. The weight of roots under swards of three *Agrostis* spp. was reported by Bell and De France (1944) to be increased after several years' application of potassic fertilizers. No significant differences existed between the pH of the soil from the different swards.

Other Elements

A high concentration of calcium carbonate in sand was found by Naylor (1939) to delay the germination of seeds of *Poa pratensis*, but thirty-five days after planting, the average length of the root system produced by plants growing in the presence of calcium carbonate was almost twice as great as that produced by plants growing in its absence. This may, however, have been partly a pH effect as the sand culture with calcium carbonate had a pH of 8·0, and that without calcium carbonate, 5·6. In further experiments with *Agrostis palustris*, Reid (1933a) found that increasing quantities of calcium in the nutrient solution caused an increase in the weight of roots and shoots produced after three months' growth. This was particularly evident in plants grown in a greenhouse, compared with those grown in the open. With plants in the greenhouse, the percentage of the plant's weight in the roots tended to increase with increasing levels of calcium, but this again was not so well marked in the results from plants grown in the open. The roots produced by 'low'-calcium plants were considerably coarser and less branched than those of the 'medium'- and 'high'-calcium plants.

In similar experiments, Reid found that the root- and shoot-weights, as well as the percentage of the weight in the roots, of plants grown in the greenhouse increased with increasing levels of magnesium in the nutrient solution. In plants grown in the open, the opposite effects, but to a lesser degree, were observed. The amount of sulphur in the nutrient solution did not influence growth to any great extent.

Combination of Elements

The effect of any compound fertilizer would be expected to depend upon the manurial elements contained in it and their proportions.

The effect of a dressing of an NPK fertilizer has been reported to vary with the intensity of the defoliation treatment to which the plants were being subjected; under lenient defoliation treatments the root- and shoot-growth increased, the shoot growth to a greater extent than the root growth, but under severe defoliation treatments the fertilizer had little or no effect. This, Lovvorn (1944, 1945) found, working with plants of *Poa pratensis*, *Cynodon dactylon* and *Paspalum dilatatum* growing in pots in a greenhouse. In the same experiments plants of *Axonopus affinis* were little affected by the fertilizer treatments. A similar interaction was found by Weinmann (1944) (Table 28) working in the field with species native to the South African highveld. It is possible that a similar interaction may occur with a nitrogen fertilizer (pp. 109–111).

Hall, Meredith, Murray and Altona (1948) working in South Africa over a period of years found that NPK and NP fertilizers increased both the root- and rhizome-weights of a sward of *Cynodon dactylon*; the shoot growth was increased to an even greater extent. A P fertilizer alone had no effect. Similar results were obtained by Weinmann and Goldsmith (1948) with the same species. Working on the highveld in South Africa, Weinmann (1943) found that under moderate defoliation treatments a PK fertilizer had a depressing effect upon root weight, and did not affect shoot growth, while an NPK fertilizer increased the shoot growth but had little consistent effect upon root weight (Table 54). These results would appear to indicate that N is frequently the most active component of a compound fertilizer.

TABLE 54

Weight of shoots produced during two seasons, weight of roots at the end of the second season and weight of roots expressed as a percentage of the total weight of shoots plus the weight of roots on Transvaal highveld. Weights in grams dry matter per 2 square-metre quadrat

(*Weinmann*, 1943)

Fertilizer	O			PK			PK + $(NH_4)_2SO_4$			PK + $NaNO_3$		
Number of clippings per year	Shoots	Roots	Percentage of the plant's weight in the roots	Shoots	Roots	Percentage of the plant's weight in the roots	Shoots	Roots	Percentage of the plant's weight in the roots	Shoots	Roots	Percentage of the plant's weight in the roots
1	930	583	39	889	418	32	1805	556	24	1848	592	24
2	1004	483	33	825	385	32	1660	433	21	1980	567	22
4	835	286	26	861	256	23	1679	448	21	1586	366	19
8	688	204	23	692	217	24	971	177	15	1051	204	16

Bronzova (1940) in Russia found that plants of *Phleum pratense* and *Bromus inermis* had their root weights increased by applications of an NPK fertilizer. These plants were defoliated once to five times per year. Laird (1930) reported that an NP fertilizer increased the root weights of *Cynodon dactylon* and *Eremochloa ophiuroides*. The swards in this experiment were subjected to intensive defoliation. Willard and McClure (1932), however, found that a dressing of an NPK fertilizer in the spring decreased the root weight and increased the herbage production of a sward of *Poa pratensis* which was regularly defoliated. The effect was greatest in spring and decreased as the season progressed. Weinmann (1948c) reported that an NPK fertilizer had only a slight effect upon root weights under both heavily grazed and moderately grazed highveld.

An increased relative concentration of roots in the upper layers of the soil as a result of application of fertilizer has been noted by some workers. Jacques (1943) (p. 112) found that this occurred as a result of applications of superphosphate to the seed-bed while Goedewaagen (1952) stated that it occurred as a result of applications of nitrogenous fertilizers, but not as a result of applications of potassic fertilizers. The application of PK fertilizer to the seed-bed followed by the application of a nitrogenous fertilizer later was found by Hughes (1937) to increase the weight of roots in the 0–4 in. soil layer under a *Poa pratensis* sward, but not to affect the roots in the 4–12 in. layer. Surface applications of NPK fertilizers were found by Haynes (1943) to increase the weight of roots under a sward of *Poa pratensis* and *Agrostis* spp. in the 0–1 in. layer of the soil, but not to affect the weight in the 1–2 in. layer; the weight in the 2–3 and 3–4 in. layers was decreased. In these three experiments the weight of roots as a whole was increased by the fertilization. Fitts (1925) noticed a similar distribution of roots of *Poa*, *Agrostis* and *Festuca* spp. due to fertilizer treatment, but the weight of roots was not given in his paper. No consistent trend could be found in the results of Sprague, H. B. (1933) concerning the effect of nitrogenous fertilizers on *Agrostis palustris*.

Chemical Composition of the Growth Medium

Previously in this chapter the experiments discussed were those concerned with the effect of applications of minerals of known form and quantity to the growth medium. It is now proposed to consider the actual composition of the growth medium.

Sprague, H. B. (1933) found that the application of fertilizer which changed the available phosphate status of the soil did not affect the weight of roots under swards of *Agrostis* spp., provided that the pH remained constant. In other experiments, application of fertilizers which increased the available phosphate status also increased the pH; this was accompanied by a decrease in root weight compared with the control plots. Sprague explained this as being due to the higher pH being more favourable to the decomposition of the old roots. Correlating the available phosphate content and the root weight of samples of soil from under a *Poa pratensis* sward, Haynes (1943) found no significant relationship on plots where a fertilizer

containing phosphate had been applied, but found a significant positive correlation in the upper 2 inches of the plots where no fertilizer had been applied. No significant correlation was evident at the 4–6 in. depth.

Working with *Agrostis* spp. in plots receiving different fertilizers, Bell and De France (1944) concluded that there was no clear-cut relationship between the root weight and the amount of phosphate in the soil. The pH apparently varied only slightly. The soil from plots receiving a high nitrogen fertilizer contained less available phosphate than did similar plots not receiving the nitrogen, which Bell and De France attributed to increased growth caused by the nitrogen resulting in the increased use of phosphorus. The quantities of available phosphorus under the swards of three *Agrostis* spp. were the same in the 1–3 and 5–7 in. layers but varied in the 3–5 in. layer, suggesting that the species concerned varied in their ability to extract phosphates from that soil layer.

The above experiments were concerned with changes in one soil type brought about by fertilizer treatment. Kmoch (1952) studied 150 grass fields in Germany on several soil types, and found no relationship between the amount of P_2O_5 in the soil and the root weight, but found a positive correlation between the phosphate requirement of the soil and the root weight. This latter is probably a pH effect similar to that of Sprague's. *Poa pratensis* was found by Fox, Weaver and Lipps (1953) to be deep-rooting in a Judson soil which had a favourable nutrient status at all depths, but to be shallow-rooting in a Carrington soil which was deficient in available phosphorus in its subsoil. Exchangeable potassium and nitrogen may also have been factors limiting root development in the latter soil.

Apparently the amount of available phosphorus in a soil may be a factor limiting root growth, but its effect may be masked by that of the soil pH.

Correlating the root weight and available potash in samples of soil from under a *Poa pratensis* sward, Haynes (1943) found that there was a positive relationship. This relationship was statistically significant in the 4–6 in. soil layer, but was non-significant in the 0–2 in. layer. Haynes concluded that potash may be a factor limiting root development where supplies of this compound are limited, e.g. in the lower layers of the soil. Kmoch (1952) in his survey of German grass fields found no relationship between root weight and soil K_2O. Limited root development of prairie grasses in the upper horizon of a Butler soil was found by Fox, Weaver and Lipps (1953) to be associated with a low content of exchangeable calcium and nitrogen.

CHAPTER 22

INTERACTION BETWEEN PLANTS GROWING TOGETHER

Under natural conditions, competition takes place between plants when they make demands on the water, light and nutrients in excess of the supply. Competition is more intense between species with the same growth form than between those which are dissimilar (Weaver and Clements, 1938). Alternatively, one partner in an association may influence the factors affecting growth to the benefit of the other partners.

Associations of Grasses of the Same Species

Within certain limits the higher the density of the population the smaller is the individual plant. De Peralta (1935) sowed seeds of *Holcus sorghum sudanensis* at rates varying from three times to half the normal rate. The plants competed for water, light and possibly nutrients. Examinations of the plants after the seedling stage but during their maiden year showed that the weight of roots per plant varied inversely with the rate of seeding, and thus the density of the population. Similar results were obtained by Nedrow (1937) in an experiment with the same species, by Nowotnówna (1937) with *Lolium perenne* and by Troughton (1956) with *Lolium perenne* and *Phleum pratense*. In De Peralta's experiments, the volume of roots per plant and their depth and spread also varied inversely with the plant density. According to Pavlychenko (1942), spaced plants of three species (*Agropyron cristatum*, *A. pauciflorum* and *Bromus inermis*) had a deeper root system and a greater number of roots which were more highly branched at all stages of development than had similar plants in a sward.

If the results of De Peralta and Nedrow are examined on the basis of roots per unit volume of soil, then, in the initial stages of plant development, the soil with the highest plant density contained the greatest weight of roots, but, in the later stages, the root weight showed no consistent trend. In Nowotnówna's and Troughton's experiments the higher the density of population the greater was the weight of shoot and root per unit area of soil.

In Nedrow's experiment, the plants were competing for both light and water, or for only one of these. The smallest root weights were produced when the competition was for both light and water, and the greatest when competition was for light only.

In both Nowotnówna's and Troughton's experiments, increasing the density of the plant population resulted in a higher percentage of the plant's weight being in the roots. Troughton was able to show that this was due to factors affecting the growth of the plants when they were very small. The distribution of the plant's weight between root and shoot was not affected by the density of the population as such in the experiments of De Peralta and Nedrow, but both found that competition for water increased the percentage of the plant's weight in the roots, while Nedrow found that competition for light had the opposite effect. The observations with regard to water and light are in accord with those made on other crop plants (Weaver, 1926).

Associations of Grasses of Different Species

The growth of four grasses (*Agrostis alba*, *Phleum pratense*, *Poa compressa* and *P. pratensis*) when grown in pure (i.e. one species) and in mixed cultures of two species was measured by Ahlgren and Aamodt (1939). The density of population was the same in all cultures and the mixed cultures consisted of 50% of each species. After five month's growth from transplanting as seedlings, the plants grown in mixed cultures were found to have produced less roots and herbage than those grown in pure cultures. The variations in the distribution of the plant's weight between root and shoot did not show any consistent trends. Ahlgren and Aamodt attributed this result to 'harmful root interactions'. Three similar experiments were conducted by Donald (1946) who measured herbage yields only. No reduction in herbage yield occurred due to associated growth, so the conclusion of Ahlgren and Aamodt is doubted by Donald.

Part of an experiment by Åberg, Johnson and Wilsie (1943) was very similar to those of Ahlgren and Aamodt and of Donald. After seven

month's growth from seed, there was no significant difference in the weight of roots per unit volume of soil due to the growth in association. Plants of *Dactylis glomerata* and *Phleum pratense* gained in root weight when grown with *Bromus inermis* but the latter had its weight of roots reduced so that the balance was maintained. Likewise, the balance of shoot growth was maintained while the variations in the distribution of the plant's weight between root and shoot showed no particular trends. These workers concluded that there was no evidence of either mutually beneficial or antagonistic associations, the responses being of the 'compensating' type.

In an experiment described by Troughton (1956) plants of *Lolium perenne* were slightly but consistently smaller when grown in a mixture with plants of *Phleum pratense*, while the plants of *Phleum pratense* were correspondingly larger. The *Lolium perenne* plants had a lower percentage of their weight in the roots, and the *Phleum pratense* plants a slightly higher percentage when grown in a mixture than in pure culture. These differences were due to differences in the relative growth rates of the root and shoot.

The 'layering' of the roots of different species when grown together has been noted by Weaver and Clements (1938) under prairie conditions; and by Linkola and Tiirikka (1936) in a dry meadow. Competition for water took place in both environments and the 'layering' of the roots would reduce the intensity of the competition (p. 78).

Associations of Grasses and Legumes

The relationship between grass and legumes grown together is made up of two parts; competition between the plants for water, light and nutrients and the availability to the grass of the nitrogen 'fixed' by the legume. The availability of this nitrogen to associated crops is not fully understood. Nitrogenous excretion from the roots of legumes under field conditions is apparently rare. It is possible that nitrogen may only become available when mineralisation of the root tissue has taken place, in which case it is possible that the experiments discussed here were of too short a duration for the legumes to provide the grasses with any nitrogen. Further references to the mechanism by which nitrogen is made available to companion plants may be found in Virtanen (1938) and Whyte, Nilsson-Leissner and Trumble (1953).

Two greenhouse studies have been carried out in America on the growth of grasses and legumes grown separately and in mixed cultures of one grass and one legume (Roberts and Olson, 1942; Åberg, Johnson and Wilsie, 1943). In each experiment the plant density was constant throughout and the mixed cultures consisted of an equal number of grass and legume plants. The plants were grown from seed in a greenhouse and examined in one case after four month's growth (Roberts and Olson) and in the other after eight month's growth. The data obtained from both experiments were difficult to interpret. Both showed a general trend in that no cases were observed in which both the grass and the legume benefited or were injured by associated growth, the responses of the plants being of the 'compensating' type. The increase in growth was usually made by the most vigorous, and the decrease by the least vigorous, of the partners. This conclusion also applied to the growth of two grasses in association in the experiment of Åberg, Johnson and Wilsie. Roberts and Olson were of the opinion that the gains in weight per unit area of soil observed in some mixtures compared with pure cultures resulted from the spreading over a greater soil area of plants with more vigorous growth habits, thus making more efficient use of the total area involved. The variations in the distribution of the plant's weight between root and shoot showed no consistent trends in either experiment.

In Roberts' and Olson's experiment, the quantity and percentage of nitrogen in the grass roots was usually increased by the associated growth of a legume and the quantity in the roots of a mixed association was usually greater than in the roots of the same species grown separately.

The results of Jacques (1943) indicated, with plants grown in pipes, that in most cases an overall smaller weight of root and herbage, especially of roots, was produced by a mixed culture of *Trifolium repens* and *Lolium perenne* or *Dactylis glomerata* than a similar proportion of plants grown in pure culture. The presence of *Trifolium repens* plants in contact with *Dactylis glomerata* consistently lowered the number of roots produced per tiller, whilst with *Lolium perenne* this was evident in two out of three seasons.

The dry-matter yield of plants of *Lolium perenne* was found by Nowotnówna (1937) to be considerably increased after 13 weeks' growth by the presence of inoculated plants of either *Pisum sativum*, *Trifolium pratense* or *Ornithopus sativus* in a medium of sand to which no nitrogen had been added. The presence of plants of *P. sativum* caused the greatest increase and the presence of *O. sativus* the least. The plants of *T. pratense* and *O. sativus* increased the shoot growth of the *L. perenne* plants rather more than the root growth. All the roots of the *L. perenne* plants growing with *P. sativum* were long and well developed and there was little interpenetration of the roots of the two species, while in the *T. pratense* series there was extensive interpenetration of the roots. In the cultures with *O. sativus* the roots of the grass plants were badly developed and short. The amount and percentage of nitrogen in the whole of the grass plants was increased by the presence of either of the leguminous species.

In a mixed culture in Nowotnówna's experiment the population of a pot consisted of ten plants of *Lolium perenne* and an equal number of plants of the leguminous species while the pure cultures consisted either of ten or twenty plants of *L. perenne*. The grass plants in the mixed cultures were larger than those in either of the pure cultures, and so the quantity of dry matter produced by the grass plants was greater in the mixed than in the pure cultures.

In an experiment in which the plants were grown in soil, Troughton (1956) found that, during 22 weeks growth from seed, one plant of *Trifolium repens* in a pot with 2 or 6 plants of *Lolium perenne* or *Phleum pratense* did not affect the growth of the grass plants.

Russian workers have stated that a mixed sward of grasses and legumes produced more roots and added more organic matter to the soil than did a pure sward of either (Suchalkina and Kotlyarov, 1949; Ivanov, 1950; Duhanin, 1940). This increase in the weight of roots was also found in the experiment of Åberg, Johnson and Wilsie, but not in Roberts' and Olson's experiment, when the results are compared on a unit area basis. A combination of *Melilotus alba* and grasses was found by Schwendiman, Hafenrichter and Law (1953) to produce more roots per acre than *Melilotus* alone, the actual quantity of roots depending on the grass species. This is in agreement with the results of Roberts and Olson.

Associations of Grasses and Trees

It appears that when grass and trees are grown together the roots of the grasses are mainly found in the upper layer of the soil, while the tree roots mainly occupy the lower layers. Competition for water and nutrients does, however, take place between the tree- and grass-roots.

Rogers (1932) in England reported that the roots of an apple tree were found mainly in the soil layer 50–90 cm. deep, while the accompanying grass roots were found mainly in the 0–50 cm. layer. Later, Rogers and Raptopoulos (1945) found that the roots of 2-year leys grown as cover crops in an orchard were mainly concentrated in the upper 6 inches of soil while about 70% of the fibrous roots of the accompanying apple trees were more than 12 inches deep.

The various reports of the modification in the positions tree roots occupy due to the accompanying grass are not in complete agreement. Howard (1925) as a result of his exposures of the roots of tropical fruit trees in Central India came to two conclusions, the first being that the trees grown with grass and those grown with clean cultivation were both able to form deep root-systems and to make use of moisture and minerals in the lower soil layers. The second was that trees grown with grass formed a very weak superficial root system and produced few active rootlets in the surface soil compared with the trees grown with clean cultivation. The results of Frith (1952) working with citrus trees in Australia showed that trees growing with a sod of unstated 'weed' species had greater root lengths in the upper 20 cm. of soil than had those trees grown in cultivated or bare ground. Oskamp (1916) found that, while the root system of trees under sod was similar to that under cultivation, the spread was one-third less, as was also the spread of the canopy. He also observed that, under the sod treatment, there appeared to be more fibrous roots in proportion to the weight of the whole root system. Beckenbach and Gourley (1932) and Baker, C. E. (1944) were both unable to find any difference in the root systems of fruit trees under sod or under cultivation.

The fact that competition does occur between grasses and trees growing together is shown by the work of Watt and Fraser (1933). In considering the relationship between *Deschampsia flexuosa* and *Pinus silvestris* growing together, they found that

if the tree roots did not compete with the grass in the upper 13–18 in. of the soil, then the growth of the grass increased. This indicates that the roots of the trees and the grass did not operate in entirely different layers. Watt and Fraser, therefore, doubted the common statement, e.g. Lindquest (1931), that trees and their accompanying herbs are edaphically complementary.

The competition between grass and trees has considerable importance in orchard management. Bedford and Pickering (1914) noticed that when an orchard was undersown with grass, the growth of the trees was arrested, sometimes with fatal results to the trees. This they attributed to a toxic substance excreted by the grass. Howard (1925) noticed a similar effect upon fruit trees in India. He suggested that the harmful influence of the grass acted in two ways; by restricting the aeration of the surface roots during the monsoon and by reducing the supply of combined nitrogen throughout the whole year. The harmful effect of lack of aeration was due to excessive amounts of carbon dioxide rather than to lack of oxygen.

More recently, work has been carried out at East Malling Research Station into the value of various cover crops for orchards. Rogers and Raptopoulos (1945) reported an experiment on the relative values of some short-term cover crops. During their growth the cover crops caused a check to tree growth but when they were ploughed-in they had a stimulating effect. This was probably due to competition for both nutrients and water, as manures were deliberately withheld. The check and stimulation varied with the cover crop, being greatest in both cases with a ley composed of *Lolium perenne* and *Lolium multiflorum*, as compared with leys composed of the *Lolium* spp. plus *Trifolium pratense*, *T. pratense* alone and a 'weed' ley.

In a later paper, Rogers, Raptopoulos and Greenham (1948) stated that grassing down with long leys resulted in a relative nitrogen shortage. Greenham (1952) has suggested that water competition may well be a feature of young swards, as, in established grass, rain may pass through the top layers of the soil, presumably through channels formed by grass roots and earthworms, to lower zones without wetting the surface to field capacity, while in cultivated soils, and presumably young swards, a high proportion of the moisture remains in the upper layers of the soil and is lost by evaporation without ever becoming available to the tree roots.

An initial check to the trees when an orchard is grassed down appears to be inevitable, due to competition for water and nitrogen, but a properly managed sward of suitable species, i.e. one which offers little competition to the trees, can produce beneficial effects, e.g. less pre-harvest drop, better fruit colour and a lessening of the severity of symptoms of mineral deficiency (Greenham, 1952).

In India, Howard (1925) found that forest trees were not only able to thrive when growing with grass, but were able to vanquish it if allowed free competition. This he attributed to the power of the surface roots of forest trees to resist the effects of an atmosphere rich in carbon dioxide, a respect in which the roots of different species varied greatly. Both Weaver and Kramer (1932) and Richardson, S. D. (1953) have reported that the growth of young trees is reduced when they are growing in competition with grasses.

Associations of Grasses and Other Plants

An experiment was reported by Hase (1941) on the difference in root development of two grass species grown in plots containing weeds and in weed-free plots. The weeds reduced the depth, spread and length of the roots. Kurtz, Melsted and Bray (1952) conducted experiments with *Zea mays* grown in slits in a grass sward. Provided that adequate nitrogen was supplied, the maize produced yields 80–100% of those obtained by conventional systems. The need for nitrogen is of interest in connection with the work on fruit trees and grass (pp. 118–9). Experiments with *Rumex confertus* by Rabotnov and Almazova (1954) indicated that interference with the growth of young plants in meadows by other species was due not to overshading but to root competition.

Several species of plants are semi-parasitic on grasses. These parasites retain the power of photosynthesis and are usually able to complete their life-cycle, which is frequently annual, without the aid of a host if necessary. The root system of the parasite, which is only slightly developed, becomes attached at certain points to the roots of grasses by minute disc-like haustoria. From these haustoria, processes penetrate into the vascular system of the host. Certain of these

semi-parasites, e.g. *Bartsia odontites*, have numerous hydathodes to enable excess water taken from the host to be released (Fritsch and Salisbury, 1944). Parasites of this nature occur in the genera *Striga* (Saunders, 1933; Wild, 1954), *Sopubia* (Kumar, 1938), *Bartsia* (Fritsch and Salisbury, 1944), *Euphrasia* (Fritsch and Salisbury, 1944), and *Pedicularis* (Fritsch and Salisbury, 1944). These semi-parasites may not be specific to the Gramineae (Andrews, 1947).

PART III

THE EFFECT OF THE PLANT UPON THE SOIL

CHAPTER 23

SOIL ORGANIC MATTER

Grass plants add organic matter to the soil while they are living by the decay of old roots and shoots and when they are ploughed-in by the decay of the whole plant. These organic materials are eventually mineralised by micro-organisms.

Decomposition

The factors concerned with the decomposition of plant residues in general have been reviewed by Waksman (1927) and Russell, E. J. (1950).

The physical condition of grass roots and rhizomes undergoing decay was followed by Weaver (1947), who found that the percentage of coarse material declined while the percentage of fine materials increased as decay progressed. Little loss in weight of the plant material occurred in the first year, but it was large in the second and third years. Any original differences in weight of material provided by different species was obliterated by the rapid loss in weight. The amount of undecayed material remaining after 3 years did, however, vary with the species. Young roots decayed rapidly and usually disappeared within 2 years. This was under prairie conditions.

The rate of decomposition of grass roots detached from the rest of the plant has been measured under controlled conditions by mixing the roots in known proportions with soil and then measuring either the rate of carbon dioxide production (Doughty, 1941; Ward, 1949) or oxygen absorption (Robinson and Jacques, in press) as a criterion of the rate of decomposition. Both Ward, studying the roots of *Poa pratensis*, *Panicum virgatum*, *Andropogon furcatus* and *Sorghastrum nutans*, and Robinson and Jacques studying those of *Lolium perenne* and *Dactylis glomerata*, reported that the maximum rate of decomposition occurred the first day after the experiment had started. The roots of *Lotus corniculatus* and *Lespedeza sericea* were stated by Ward to reach their maximum rate of decomposition on the second day but the legumes in Robinson and Jacques' experiment (*Trifolium repens* and *Trifolium pratense*) reached their maximum on the first day, as did the grasses. The roots of *Festuca rubra* were found by Robinson and Jacques over a period of two months to break down more rapidly than those of *Lolium perenne* or *Dactylis glomerata*. Ward found that over a period of twenty-three days the shoots of *Poa pratensis* decomposed far more rapidly than did the roots which decomposed at approximately the same rate as the roots and shoots of the other grasses in the experiment which all decomposed at approximately the same rate. *Lotus corniculatus* and *Lespedeza sericea* resembled *Poa pratensis* in the difference in the rate of decomposition of roots and shoots.

As with other plant residues, the nitrogen supply appears to be one of the major factors concerned in the decay of grass roots and the one most frequently investigated. Under controlled environmental conditions, Doughty (1941) showed that the rate of decomposition of the roots and leaf bases of three grass species was comparable with their carbon/nitrogen ratios; the more rapid the decomposition, the narrower the ratio. This is also true of other plant materials (Waksman, 1927). During decomposition, the roots of grasses have been shown to remove more nitrogen from the soil than do those of clovers, which presumably have a narrower carbon/nitrogen ratio (Lyon, Bizzell and Wilson, 1923). Denitrifying bacteria

have been stated to be especially characteristic of decomposing graminaceous roots, while those decomposing cellulose are characteristic of leguminous roots (Krasiljnikov and Nikitina, 1945).

The presence of decomposing grass roots in a soil may result in a nitrogen deficiency to the growing crop. Sorghum is well known to have a depressing effect upon the succeeding crop (Russell, E. J., 1950). This has been shown by Conrad (1927, 1932, 1937, and 1938) to be due to the high sugar-content of the crown roots. When sorghum is ploughed up there occurs an extremely rapid increase of the non-nitrifying bacteria which utilise the available soil nitrates to the detriment of the growing crop. Unfavourable soil structure for plant growth may also ensue during the decomposition of the sugars. These ill effects may be overcome by taking a leguminous crop just before the sorghum is grown, or by adding nitrates to the soil.

Decaying roots of *Bromus inermis* have been shown to cause a similar nitrogen deficiency. Myers and Anderson (1942) grew six species of temperate grass and *Medicago sativa* in soil which had previously grown *Bromus inermis* and still contained all the old roots. The herbage yields were lowered by the *Bromus* soil but the equivalent of 200 lb. of sulphate of ammonia per acre more than overcame any deleterious effect. Prior to this experiment Benedict (1941b) had stated that the presence of dead roots of *Bromus inermis* in the sand greatly decreased the growth of both the roots and the herbage of the same species when grown in sand culture, even though an abundant supply of nitrogen was available. Benedict attributed this result to a toxin derived from the dead roots. Myers and Anderson questioned Benedict's conclusion as they could find no evidence of a toxin.

The importance of nitrogen in the process of decay is shown by other work. Gel'tser (1945) reported that inoculation with bacteria of the legume component of a ley caused a 50% increase in the production of 'active' humus. Soils containing undecayed root fibre of *Agropyron cristatum* were stated by Lehane and Staple (1943) to have a wide carbon/nitrogen ratio which narrowed as the root fibre decomposed. In England, observations have shown that an application of nitrogenous fertilizer is essential to the establishment of the sown species in the direct re-seeding of an old turf (Martin, A. E., 1949). It would appear that micro-organisms concerned in the decomposition of grass roots are able to utilise soil nitrogen and to acquire this nitrogen in competition with, and to the detriment of, the growing crop.

It might be assumed on the basis of the carbon/nitrogen ratio that the roots of leguminous plants, which one expects to contain a high percentage of nitrogen, would decompose far quicker than those of grasses. In experiments in which the rates of decomposition of detached roots were measured (p. 121) Robinson and Jacques (in press) found that the roots of legumes did actually decompose more rapidly than those of grasses but Doughty (1941) and Ward (1949) found that they decomposed at the same rate as those of grasses. This difference in experimental results may be due to differences in species, experimental conditions or to the age of the roots as Robinson and Jacques found that roots of *Trifolium repens* and *T. pratense*, obtained four months after sowing, broke down more rapidly than those obtained twelve months after sowing.

For the rapid decomposition of plant material the pH of the medium should not fall too low, otherwise the microbial activity becomes unduly restricted (Russell, E. J., 1950). The decay of a 'meadow sward' in Germany was found by Böhler (1940) to be more rapid when the soil pH was above 6 than when it was below this figure. The process of decomposition lowered the soil pH. If the soil pH was below 6, an application of lime was necessary for the maximum growth of the following crop. For the conditions found in Ceylon, i.e. high temperature and rainfall, which promote the rapid decomposition of soil organic matter, Haworth (1953) has suggested that the value to a succeeding crop of a large quantity of grass roots in the soil lies in their provision of a supply of readily available nutrients, not in the addition of organic matter, as such, to the soil.

Crider (1945) has shown that the percentage of lignin in the roots of *Eragrostis curvula* increased with the age of the plant, from 9·69% in the first year to 20·20% in the third. Lignin is one of the slowest of plant constituents to decompose (Russell, E. J., 1950) so it would be expected that the rate of decomposition of the roots of this species would decrease as the plants aged. This was found by Robinson and Jacques (in press) to be so for the roots of *Trifolium repens* and *Trifolium pratense*. Slowness of decomposition of

the roots was considered by Crider (1945) to be an asset in grasses planted for erosion control.

The slowness of decomposition of organic matter derived from leys has been stated to be a problem in Russia. The organic matter accumulated in the Stony Steppe after a one-year ley was found by Suchalkina (1951) not to have decomposed completely 5 years later. Duhanin (1940) reported that, in dry conditions, a large proportion of the plant residues remained undecayed three years after ploughing up a ley, causing subsequent crops to be deprived of about 50% of the nitrogen and phosphorus which the original residues contained. In order to achieve rapid decomposition he makes several recommendations which are aimed at moisture conservation and the growth of fine roots, especially of *Medicago sativa*, which are stated to decompose quicker than coarse ones.

The decomposition of roots of grasses and herbs were reported by Lagunova (1952) to cause a marked decrease in the proportion of adsorbed sodium in solonetz soils, and a corresponding increase in the proportion of calcium and magnesium derived from the root material and carbonates formed from the carbon dioxide evolved in decomposition. From this, Lagunova concluded that the vegetation plays a part in the desalinising of saline soils.

A possible role played by decomposing grass roots in the formation of clay minerals was suggested by the work of Aidinyan (1954). In the Stony Steppe of Russia he found that the magnitude of the $SiO_2 : R_2O_3$ ratio (R representing aluminium and iron) in living and dead roots decreased with increasing soil depth, particularly in mown steppe. The chief mineral elements in the A_1 horizon were silica, calcium, and aluminium or magnesium, followed by potassium, phosphorus and iron, whereas, in the A_2 and B_1 horizons, calcium minerals predominated. Manganese oxide occurred in all horizons. Calculations showed that the minerals were accumulated in the upper horizons where the greatest amounts of root occurred. The processes of leaching, decomposition and mineralisation of dead vegetation resulted in a relatively great accumulation of aluminium and iron which, together with other minerals, may have enabled new clay minerals to be synthesised. This synthesis of secondary clay minerals would explain the small $SiO_2 : R_2O_3$ ratio found in the fine fractions of soil.

Relationship between the Quantities of Roots and Soil Organic Matter

In a well-drained soil the quantities of both soil organic matter (Robinson, 1949) and of grass roots decrease with depth. Weaver, Hougen and Weldon (1935) found that in two prairie soils the amount of roots decreased more rapidly than that of soil organic matter. In the profiles of these two soils (to a depth of 5–7 feet), the ratio of total soil organic matter (including roots) to the organic matter of the roots was roughly a linear function of depth, except in the upper six inches where the proportion of the plant materials to soil organic matter was increased by the presence of a large amount of living roots and rhizomes and by the favourable conditions for decomposition of dead material. Similar relationships were found to exist between soil and root nitrogen. In one of the profiles examined, at certain horizons excessive water had caused conditions unsuitable for decomposition resulting in a departure from the linear function. Sprague, H. B. (1933) working with the upper nine inches of soil was unable to establish a relationship between the soil organic matter and the root distribution of three species of temperate grasses after four to five years' growth.

Slight correlations have been recorded between the root weight and soil organic matter of different swards. Sprague, H. B. (1933) studied the effect of several fertilizer treatments, after 6 years, on a sward of *Agrostis palustris*. In one experiment, no correlation was found between the root weight of the swards and the soil organic matter, but, in another, a positive correlation of minor magnitude was established but was attributed by Sprague to experimental error. More recently, Gist and Smith (1948) found that broad differences in the soil organic matter in the upper three inches could be attributed to differences in the root growth of five grass species in their third harvest year. Close correlation was not possible and no correlation was found below this depth. Sprague took his results to indicate that root development is little influenced by the organic-matter content of the soil but rather that soil organic matter is dependent upon root occupation. Shively and Weaver (1939) showed that in three out of five areas of the prairie of Nebraska and the surrounding States a strong positive correlation existed between the quantities

of plant materials, organic matter and nitrogen in the soil. The lack of correlation in the other two areas they attributed to sampling errors.

Effect of Grass Plants upon Soil Organic Matter

It has been shown in most countries of the world that grass increases the organic-matter content of the soil, e.g. in Europe by t'Hart (1950) and Gisiger (1950), in America by Carlson (1922), McHenry and Newell (1947) and White, Holben and Richer (1945), in Russia by Černy (1938), Vorobieva (1939) and Suchalkina and Kotlyarov (1949), in Ceylon by Joachim and Kandiah (1944), and in South Africa by Theron and Haylett (1953). The organic matter in Swiss grassland soils has been reported to be more concentrated in the upper 12 cm. than in the arable soils (Gisiger, 1950). The ploughing-in of a sod has been shown to increase the organic matter still further. (Iljin, 1949).

For Russian conditions, Ivanov (1950) has stated that perennial grasses are active humus accumulators, compared with annuals, partly because of their much greater root systems and partly because they die off in late autumn and are protected from decomposition during the winter.

Hedrick (1948) stated that the organic-matter content of Californian range soils varied inversely with the intensity of grazing, as the weight of the root system would be expected to do. Lopato and Sidorov (1941) found that the organic-matter content of soil taken from directly underneath plants grown in rows was higher by 2–3% than that of soil from the inter-row spaces.

'Mat-Formation' and the 'Sod-Bound' Condition of the Sward

The formation by a grass sward of a mass of root and rhizomatous material on the top, and in the upper few inches, of the soil is well known. If the material is mainly above ground, then it has been called a 'mat' (Orr, 1928; Davies, 1939; Bates, 1948), but if mainly below ground, then the sward has been termed 'sod-bound' (Myers and Anderson, 1942). These conditions seem to be associated with factors which limit the decomposition of organic matter in the soil. Several workers have considered a lack of nitrogen to be the chief causative factor. Davies (1939), in the Falkland Islands, found that a mat would decompose on the addition of a nitrogenous fertilizer. The lack of nitrogen was explained by Theron (1951) as being due to the action of the grass roots on the nitrate-forming organisms in the soil (see p. 70). In Great Britain, mat formation has been associated with acid soil conditions (Stapledon and Hanley, 1927) and with lack of earthworm activity (Richardson, H. L., 1938), the latter probably being a result of the former.

Both mat formation and sod-binding are complementary to a decrease in herbage yield. This Bates (1948) considered to be due to crowded conditions in the soil as a result of the excess organic matter and consequent lack of plant vigour. Benedict (1941b) was of the opinion that a toxin was produced by the decomposing roots of *Bromus inermis* which inhibited further growth of the plants; but no evidence of such a toxin was found by Myers and Anderson (1942) (p. 122).

CHAPTER 24

SOIL STRUCTURE

Soil structure is usually defined as the arrangement of soil particles (Baver, 1948). A large variety of methods has been developed in endeavours to classify or measure this characteristic: Low (1954) has recently reviewed some of them. One of the most commonly used methods has been the measurement of the stability of aggregates of known size when subjected to 'wet-sieving' (Yoder, 1936; Russell and Tamhane, 1940; Low, 1954). Some discrepancies in the results reported by individual workers may be expected, due to the wide differences in the actual technique employed.

The percentage of water-stable aggregates increases in a soil which is growing a grass sward (Kurtesov, 1939; Grakhosskii, 1940; Martin, W. S., 1944; Hénin, 1944; Joachim and Kandiah, 1944; Gish and Browning, 1949; Vorobiev, 1950; Low, 1954). Soil which grows a rotation of crops, including a ley, will contain a larger percentage of water-stable aggregates than one which grows arable crops only (Gish and Browning, 1949; van Bavel and Schaller, 1950). The actual increase in the proportion of water-stable aggregates which will be produced by a grass sward will vary with the type of soil and its initial structure, the climate, the grasses in the sward (Sarakhov, 1938; Iovenko, 1939; Pavlychenko, 1942; Russell, E. J., 1950; Barley, 1953) and the age of the plants (Cyganov, 1948).

These variations have been related in various ways to the root system of the grasses. Pavlychenko (1942) showed that the soil-binding equivalent (product of the length of the root system and its tensile strength) of a species could be related to its ability to produce stable aggregates, those species with a high soil-binding equivalent producing a large number of stable aggregates. The differences in the soil-binding equivalents were, however, hardly large enough to account for all of the large variation between species in aggregate formation (pp. 10–12, 127, 128). Stevenson and White (1941) found a similar relationship between the diameter and tensile strength of the roots of a species and its stable-aggregate-forming ability. Williams (1955) and Robinson and Jacques (in press) have reported that the effectiveness of grasses and clovers in increasing the aggregate-stability decreased with depth, as did the weight of roots. Pavlychenko (1942) stated that those species with deep roots produced stable aggregates at greater depths than those with shallow roots.

Lopato and Sidorov (1941) found that when plants of *Agropyron* sp. were grown in wide rows they produced a smaller weight of roots per unit volume of soil and a smaller proportion of water-stable aggregates than when they were sown in narrow rows. Burov (1953) also reported that the extent of aggregation induced by grass/legume mixtures was proportional to the shoot-root mass. In England, Williams (1955) reported that small but consistent differences noted between swards of *Lolium perenne*, *Dactylis glomerata*, *Festuca pratensis* and *Phleum pratense* in their abilities to increase the stability of the soil's aggregates could be positively correlated with their root weight. Variations in grazing management which only slightly affected the root weight did not influence the quantity of water-soluble aggregates produced, although the herbage production varied by as much as 40%.

A significant correlation was found by Robinson and Jacques (in press) to exist between the quantity of roots produced by five species (*Lolium perenne*, *Dactylis glomerata*, *Festuca rubra*, *Trifolium repens* and *Trifolium pratense*) and the degree of soil aggregation four months after sowing, but not at later dates up to twenty months after sowing. Thus a correlation was obtained prior to the decay of any large quantity of organic material produced by the plants but not afterwards. Barley (1953) three years after sowing was also unable to find any relationship between the quantity of roots and the proportion of water-stable aggregates produced in the 0–3 in. layer of the soil by *Dactylis glomerata*/*Trifolium repens*, *Lolium perenne*/*Trifolium repens* and *Lolium perenne*/*Medicago sativa* mixtures.

In a comprehensive study with *Andropogon furcatus*, *Panicum virgatum*, *Sorghastrum nutans*, *Sporobolus asper*, *Bouteloua gracilis*, *Poa pratensis*, *Lotus corniculatus*, *Lespedeza sericea*, *Lespedeza stipulacea*, *Lespedeza capitata* and *Trifolium pratense* grown separately, Ward (1949), three and five years after sowing, found only a low non-significant positive correlation between the degree of aggregation and the weight, volume and rate

of decomposition of the roots in the 0–3 in. layer of the soil. There were much higher positive correlations between the degree of aggregation and the quantity of shoots produced and their rate of decay. In the 3–6 in. layer there were significant positive correlations between the quantity and volume of roots and the degree of aggregation. A small non-significant negative correlation was found between the degree of aggregation and the rate of decay of the roots. Certain of these results are apparently at variance with those of Robinson and Jacques (in press). They found a highly significant positive correlation between the rate of decay of the roots of *Dactylis glomerata*, *Lolium perenne*, *Festuca rubra*, *Trifolium repens* and *Trifolium pratense*, and the increase in the degree of aggregation produced by the decomposition of the roots. The difference in the results may be due to the fact that Ward measured the increase of aggregation produced by the living plant, while Robinson and Jacques measured that produced by the decomposing roots only. Other workers have reported significant correlations between the nitrogen and carbon contents of the soil under grass swards and the proportion of water-stable aggregates. (McHenry and Newell, 1947; Ackerman and Myers, 1943), the carbon and nitrogen depending to a large extent upon the decay of parts of the grass plants.

It would appear that grass roots are concerned directly in the formation of stable aggregates through their physical actions upon the soil and indirectly through their providing food for micro-organisms.

One of the earliest theories put forward to account for the formation of stable aggregates by grass roots was based on the pressure exerted by the growing root, which was thought to effect a separation of the particles adjacent to the root and to press these units together to form aggregates. In other words, each root hair that penetrated a clod introduced a point of weakness into that clod. The penetration of a sufficient number of root hairs throughout the clod caused the formation of granules (Baver, 1948). Williams (quoted by Vilensky, 1949) was of the opinion that the pressure was built up gradually by new roots growing down old root channels which contained the remains of old roots. This process continued until the channel was so completely filled with dead residues and growing roots that the pressure forced the mass to break along the lines of weakness.

Another theory put forward was that granulation was accomplished by changes in the moisture content in the vicinity of the root system as a result of water intake by the plant. This produced localised dehydration, which brought about shrinkage and the formation of surfaces of fracture (Baver, 1948). Nikolsky (1942) advanced the hypothesis that the root hairs bind the separate particles together. Small roots were reported by Ivanov (1950) to be more effective than large ones in improving soil structure. That the physical characters of roots play some part in the formation of aggregates is shown by the results of Pavlychenko (1942), Stevenson and White (1941), and Ward (1949).

Plants of *Sorghum vulgare* var. *sudanense* were found by Hubbell and Chapman (1946) to be unable to produce aggregates when grown in a sterile soil. Bacteria, actinomycetes, and fungi allowed to grow in similar media each produced a distinct type of aggregate. When these plants were grown with a mixture of these micro-organisms or with any one of them, the grass roots produced compound structures comprising microbial aggregates held together by roots. Total aggregation was not affected by the presence of roots, but the structures were larger when the roots were present. The direct action of the roots would appear, therefore, to be merely a continuation of the work of the micro-organisms which are the main influence and which, presumably, feed upon organic matter derived from the grass plants. This would account for the imperfect correlations which were obtained by Pavlychenko (1942) and Ward (1949) between the physical characters of the root systems and the degree of aggregation. The results of Ward may be interpreted as indicating that in the 0–3 in. layer, the action of the micro-organisms causing the decay of the top growth was the controlling factor, while, in the 3–6 in. layer, the binding action of the roots played a more important part.

The importance of organic matter in the formation of a stable structure has frequently been emphasised (McHenry and Newell, 1947; Ackerman and Myers, 1943). Gel'tser (1936) explained the differences between swards in the formation of aggregates as being due to differences in the rate of decomposition of the plant material added to the soil, the more rapid the decomposition

the better the structure. The more rapid decomposition would presumably increase the microbiological activity but would decrease the physical effect of the roots. Several suggestions have been made concerning the compound produced by the micro-organisms which acts as a cement in binding the soil particles together, but no general conclusion appears to have yet been reached (Russell, E. W., 1938; Russell, E. J., 1950). Kvarachelia (1951) investigated the composition of the cementing compounds by subjecting soils to successive treatments with various reagents. Treatment with benzene, which removed the resinous materials, decreased the number of macro- but not micro-aggregates. Treatment with sodium oxalate - sodium hydroxide which removed the organic colloids and dispersed the clay, resulted in the greatest disruption of aggregates. Even after these treatments were followed by Tamm's oxalate reagent and sodium hypobromite, whereby nearly all the humic matter was removed, micro-aggregates were still present on grass roots from soil samples taken from podzolic soils under grass. Gel'tser (1944) and Suchalkina and Kotlyarov (1949) have suggested that the micro-organisms in the rhizosphere converted root exudates into cementing compounds but there is little evidence to support the idea that root exudates are produced in any quantity (p. 69 *et seq.*).

To summarise, the direct action of the grass roots on soil structure appears to be the holding together of soil particles and small aggregates so that they form larger structures. Indirectly, the roots provide organic material from which micro-organisms are able to manufacture cementing substances. Many other factors influence the degree of aggregation of a soil and a great deal of data is available concerning their actions, but they are not directly concerned with the roots of grasses (Russell, E. W., 1938; Russell, E. J., 1950; Baver, 1948; Martin, Martin, Page, Raney and Ment, 1955).

The effect of grass roots upon soil structure as measured by means other than aggregate analysis has not received so much attention. Neither Barley (1953) nor Ward (1949) were able to find any relationship between the pore space and root characteristics in the upper three inches of the soil. Barley was concerned with the weight of roots and Ward with the weight, volume and rate of decomposition. Ward did, however, find a significant correlation between the volume-weight of the soil and the quantity of shoot growth and its rate of decomposition. In the 3–6 in. layer of Ward's soil there was a positive correlation between the weight and volume of roots and the pore-space. These are similar results to those obtained when the structure was measured by means of aggregate analysis.

In the 0–3 in. layer, Ward was unable to relate the permeability of the soil to any of the plant characters (weight, rate of decomposition of both roots and shoots, volume of roots) that he studied. In the 3–6 in. layer, he found a very highly significant positive correlation between the rate of permeability and the quantity of roots. This, he thought, was due to the opening up of the soil by root channels and to increased pore-space. Baver (1948) stated that increased permeability resulted from old root channels.

A negative correlation was found by Barley (1953) between the 'infiltration rate' and the quantity of roots produced by five grass/legume mixtures in the 0–3 in. soil layer. This he suggested may have been due to the plant material occupying a greater proportion of the pore-space at the higher root weights.

The permeability of the soil has been noted to increase soon after a grass sward is ploughed-in. Emerson (1954) has suggested that this could be due in part to the conduction of water through the severed grass roots. In laboratory experiments with *Lolium perenne* he found that the diameters of the conducting elements, calculated from the hydraulic data obtained by measuring the rate of flow of water through severed roots, was in close agreement with the diameters of the metaxylem elements measured in transverse section. The roots of *Lolium perenne* were found to give the most easily interpreted results as they rarely contained more than one metaxylem element, and this formed a natural capillary tube with only a few minor restrictions. The roots of *Phleum pratense* gave more complicated results as the number of metaxylem elements was not constant throughout the length of the root. The flow of water along the roots of *Dactylis glomerata* was small when compared with the roots of other species studied, because, while the roots of *Dactylis* had the largest number of elements, they were the smallest in size.

CHAPTER 25

SOIL EROSION

Several investigators have shown that the loss of soil through erosion from areas growing a sward was less than from similar areas growing tilled crops or areas without vegetation (Bennett, 1935; Weaver and Noll, 1935; Kramer and Weaver, 1936). In particular, rhizomatous grasses are very effective in protecting the soil (Carrier 1936; Jacks and Whyte, 1939).

The effectiveness of a sward depends upon (1) the action of the top growth in providing a protective covering for the soil, and (2) the roots, which increase the soil's resistance to movement and its ability to absorb water.

The value of the top growth was demonstrated by an experiment of Kramer and Weaver (1936). Using an overhead spray of water, they showed that the time taken to wash the soil away from the roots of swards from which the top growth had been removed was considerably less than from similar swards complete with top growth. The tops were relatively more effective than the roots in preventing the soil from being washed away. Species varied considerably in their capacity to hold the soil, the time taken to wash it away varying roughly with the weight of roots and tops.

Carter and Law (1948) found that the time required to wash soil away from the roots of plants varied directly with the quantity (weight and volume) of roots present. They compared six species under three defoliation treatments. Campbell (1945) obtained what he considered to be a measure of the 'binding' capacity of a plant's roots by pulling the plant up by its crown and then weighing the roots and the soil attached to them. The long and very numerous fibrous roots of his grasses permeated the soil so thoroughly that the entire mass of soil beneath the plant could be lifted bodily with little difficulty. The ratio of $\frac{\text{weight of soil}}{\text{weight of roots}}$ was, he found, very high for grasses in comparison with other plants.

The binding of the top soil by grass roots into a continuous carpet-like mat, capable of resisting violent winds and the action of water, has been remarked upon by several workers (Weaver and Harmon, 1935; Kramer and Weaver, 1936; Pavlychenko, 1942).

Dittmer (1938) considered that the ability of a species to prevent erosion depended upon the length and degree of branching of its root system, *Poa pratensis* being superior to the cereals in these respects and for this purpose. Pavlychenko (1942) was of the opinion that it depended not only upon these two factors but upon the strength of the roots as well. To compare species he used 'Soil Binding Equivalents', which he defined as the product of the length in centimetres of the roots per cubic centimetre of soil and their tensile strength in grammes. To obtain this figure for a species, the product was calculated separately for the main root and for the various orders of branches and the results summed (Table 55). Pavlychenko stated that while these values obviously vary with the age of the plants and with the localities in which they grow, nevertheless they do give certain quantitative concepts of the plants' resistance to erosion. The main roots exerted a considerable binding effect, but their chief significance rested in their ability to produce multitudes of branches which penetrated the soil in all directions and came into direct contact with the smallest soil particles. The root fibre bound the pulverized soil into larger structural units which in time became stabilized. As the soils growing swards of species with high soil-binding equivalents contained a high proportion of stable aggregates, Pavlychenko was of the opinion that there was, possibly, a close relationship between the amount and strength of the root material of a species and its ability to restore the structure of a pulverised soil. Stevenson and White (1941), however, were of the opinion that differences of the magnitude observed between the strength of roots would not account for the great differences in soil structure. Crider (1945) was of the opinion that the ability of a grass to resist soil erosion was related to the diameter and tensile strength of its roots as well as to the quantity of both the root- and shoot-growth.

The necessity for a soil to have a granular structure, such as that produced by a grass sward, if it is to withstand erosion was emphasised by Jacks and Whyte (1939). Weaver and Harmon (1935) thought that the action of grass roots in preventing erosion was due to their increasing the

TABLE 55

Soil-binding equivalents of 10 grasses

(*Pavlychenko*, 1942)

Species	Base of culm	Rhizome	Main root	Branches 1st Order	Branches 2nd Order	Branches 3rd Order	Species total
Agropyron smithii	—	576	1698	6906	211	11	9402
Andropogon furcatus	—	115	941	5856	1472	18	8402
Andropogon scoparius	—	176	714	672	198	39	1799
Bouteloua gracilis	—	—	613	1361	140	—	2114
Poa pratensis	—	92	600	1464	126	—	2282
Sporobolus cryptandrus	—	10	788	459	95	—	1352
Stipa spartea	16	—	873	3775	434	24	5122
Agropyron cristatum	46	—	1533	6899	879	24	9381
Agropyron pauciflorum	5	—	428	774	51	3	1261
Bromus inermis	—	224	1302	2237	121	—	3884

soil's humus content and aggregation, so increasing its pore-space and ability to absorb water as well as binding the soil particles together.

The management of a sward has been shown to affect its ability to resist erosion. Partial defoliation by clipping and grazing have both been found to decrease the time required to wash the soil away from the roots of a sward and to decrease the quantity of roots (Weaver and Harmon, 1935; Carter and Law, 1948). Run-off and erosion were stated by Weaver and Noll (1935) to be least from natural prairie, somewhat more from grazed pastures and most from bare cultivated ground. The effect of grazing was presumably due to its reducing the root system and possibly the ground cover.

After the breaking of a sward, the resistance of the soil to erosion apparently depends to some extent upon the resistance of the roots of the sward to decay. Pavlychenko (1942) stated that the root fibre of *Agropyron cristatum* (a species with a high soil-binding equivalent) resisted decay for three years and held the soil from erosion for six years. Roots of *Agropyron pauciflorum* (which had a low soil-binding equivalent) were largely reduced to dust within three years and failed to hold the soil even one year after the sward was broken.

PART IV

METHODS EMPLOYED IN THE STUDY OF UNDERGROUND ORGANS

Direct observation of growing roots is difficult because of the soil which surrounds them. This difficulty may be overcome by growing the plants in water culture or a nutrient mist, but how far root systems grown in this manner are comparable with those grown in soil is debatable: Rappaport (1938) (pp. 9, 10) has shown that different types of roots were produced by *Lolium perenne* plants according to the medium in which they were growing. A glass-sided vessel for measuring the growth of seminal roots whilst in culture solution was devised and used by Pollock, Goodwin and Greene (1954). Attempts have been made to study roots growing in soil by means of glass-sided panels inserted into the faces of specially prepared trenches (Rogers, 1934, 1939) and by means of boxes with glass sides (Rotmistroff, 1908; Richardson, S. D., 1953). The disadvantages of these methods of direct observation are that the field of vision is limited to those roots near the glass panels and that relatively few measurements may be made.

The other methods of study involve the separation of the roots from the soil so that, even if the plant is not killed, its growth is seriously interrupted. Numerous techniques have been devised to carry out this separation, the simplest of them being that used by Weaver (1926). A trench was dug at some distance from the plant to be studied and the roots were traced back to the plants from the face of the trench by carefully excavating the soil with hand tools. This is a very laborious procedure and is only suitable for certain experiments. A relatively large amount of soil remains attached to the roots. A modification of this method uses a spray of water to separate the roots from the soil (Upchurch, 1951).

A more complicated process consists of holding the roots in the position they occupy in the soil by means of wire supports while the washing process takes place. The final result, theoretically, is the complete root system with every root in its natural position but without the surrounding soil. One of the first workers to use this method was King (1892, 1893) who isolated a prism of soil several feet long and one foot thick by means of trenches dug round it to the maximum depth of the root system. The prism was then fitted with a cage of galvanized iron and wire-netting. When this was in place, sharpened wire were pushed through the soil of the prism in parallel rows along the meshes of the netting. Next, the loose surface of the soil was taken off and replaced by a block of plaster of Paris. Finally, the soil was removed from the cage with a stream of water from a force pump. The roots, which were held in position by the cross-wires, were photographed through the netting. Many modifications of this technique have been developed, the major one involving the transport of the soil block to the laboratory prior to washing. With this modification the sample may be soaked in water for some time prior to the commencement of the washing operation, so aiding the breaking down of the soil aggregates. The technique used by Pavlychenko (1937) involved the transport of a block of soil to the laboratory for washing without the use of supporting wires within the soil and was termed by him the 'soil block' method. This term may also be applied to similar methods.

A variation of this method was devised by Jacques (1940). A 'cage' of wood and wire was sunk into the ground before the experimental seeds were sown. Later the cage was lifted and the soil washed away. This method had the disadvantage that it disturbed the soil prior to the growth of the plant.

A widely used modification involves the use of a 'nail-board'. This is a board of wood, usually rectangular, through which nails project on one side at right angles to the major plane of the board. This board is inserted into the side of a trench so that the nails penetrate into the soil.

The soil around the board is then cut away so that a prism of soil remains attached to the nails. The board and prism of soil are then transported to the laboratory where the soil is washed away. The size of board, and the size and position of the nails have varied greatly between workers (Blaser, 1937; Goedewaagen, 1948, 1949; Salonen, 1949). The root system, when washed free from soil, may be preserved by means of treatment with cellulose, as described by Schuurman (1955) and Schuurman and Goedewaagen (1955). The frontispiece includes a photograph of a specimen prepared in this way.

With the 'nail-board' and similar methods, it is relatively easy to keep the main roots in roughly the positions they occupy in the soil but is very difficult with many of the small ones. The small roots are very apt to become detached from the main ones and so become misplaced. The roots unattached to the crown of the plants contained in the sample are very easily misplaced, if not completely lost during the washing process.

Other workers have devised techniques for separating the roots from the soil irrespective of the position the roots occupy in the soil. These methods consist essentially of taking a soil sample from the field, i.e. containing both soil and roots, soaking it in water and then washing the roots free from soil with a jet or spray of water aided by hand manipulation. The water used in the washing process drains away through a fine-meshed sieve which retains the roots and large particles of soil. These latter are separated by decantation, the roots tending to float and the soil to sink. This method differs from those previously described in that no attempt is made to retain the roots in their natural positions. A soil sample may be divided into horizons, e.g. 0–3, 3–6, 6–9 in. so that a smaller sample is dealt with in each washing operation and the vertical distribution of the roots may be described. In the uppermost horizon many of the roots will be attached to the crowns of the plants and separation of these roots from the soil by decantation may not normally be necessary as they can be washed free from soil while in bulk. Under some conditions, e.g. with dry, sandy soil, most of the soil may be removed from the roots by shaking the plants prior to washing.

The sample may consist of a single plant or of a known volume of soil. The size of sample and the tools used have varied greatly. Generally, much smaller samples than those used in the 'soil block' and 'nail-board' methods have been found to be most suitable. The types of sampling tool are legion and almost any type may be used. The auger type is not favoured as it breaks the soil and roots into fragments which are difficult to handle, as well as giving a quantity of soil whose volume is not known with great accuracy. The simplest type of sampler, other than a spade, is a cylindrical metal tube, sharpened at one end, which is knocked into the ground so that when pulled out it contains a core of soil which can be pushed out with a piston. Several modifications may be made to improve the performance of such a sampler, e.g. by tapering the cutting head externally, or by increasing the internal diameter of the tube so that it is larger than that of the cutting edge. The diameter of such tools has varied between approximately one and four inches. Jacques (1937b) has described a square sampler built on similar lines, while a rectangular sampler, with one side missing, which is pushed into the side of a trench has also been used (Könekamp, 1953). A modification of the cylindrical sampler consists of reducing the vertical height to 1–2 in. so that it resembles a ring rather than a cylinder. Samples are taken one below the other until the required depth is attained. This obviates the necessity for dividing a large sample into several horizons. A comparison of several methods of sampling on the sandy soils of Germany has been reported by Simon and Eich (1955).

The length of time during which the samples are soaked prior to washing may vary from a few minutes to three or more days. Much depends upon the soil type. The addition of chemicals—calcium hydroxide, (Bates, 1948) or sodium chloride, (Barley, 1953)—to the water in the soaking tank to aid the dispersion of the soil aggregates has been tried, but without much success when the samples were placed into the tank in a moist condition. Schuurman and Goedewaagen (1955), however, report that the washing was greatly facilitated when the samples were thoroughly dried at 105°C. and then soaked in a solution of sodium pyrophosphate (134 g. to 50 litres of water).

The root-washing arrangements vary greatly between workers. Some have washed directly over a sieve while others have carried out the actual washing in a bowl or bucket and have then poured the contents through a sieve. The disadvantage of washing directly over a sieve is that small pieces of root may be forced through the

meshes of the sieve by the water pressure. The aperture of the sieve mesh has varied from approximately 0·3 mm. to 1 mm. Some mechanical devices (Fehrenbacher and Alexander, 1955; Fribourg, 1953; Gates, 1951) have been used to carry out the washing automatically, but no critical test of these devices has yet been reported. Barley (1953) separated the mixture of soil and roots by centrifuging them in a sodium chloride solution (density 1·2 g./cc.) and filtering the supernatant liquid. Later he evolved a technique which involved the grinding of the soil to pass a 5 mm. sieve and cutting the roots into small lengths, dispersing the mixture of roots and soil in an aqueous mineral solution by means of rapid mechanical stirring and then decanting by hand (Barley, 1955).

A serious disadvantage of the washing method is that the roots cannot be completely separated from the other soil organic matter except by using the hand and eye during the washing process. This has led several workers to dispense with the term 'roots' and to substitute terms such as 'underground plant material' (Shively and Weaver, 1939), 'roots and other plant residues' (Saharina, 1940), 'root fibre' (Stevenson and White, 1941), 'macro-organic matter' (Barley, 1953). Jacques (1945) attempted to separate roots from other organic matter by allowing the water suspension in which they were contained to flow over a rubber baffle consisting of a flat rubber base from which erect rubber cones projected. These cones prevented the passage of the relatively long pieces of root, but allowed round seeds and the short pieces of other organic matter to pass.

In the washing process it is very difficult to wash the roots absolutely free from soil. To counter this it is a common practice to determine the silica content of the 'roots' and to reckon the silica as soil adhering to the roots. The silica may be determined either by ashing (Willard and McClure, 1932) or by digestion of the organic matter (Smith and Mabbitt, 1953).

Soil samples prior to washing and washed roots can be stored at a low temperature, in an aqueous solution of formaldehyde, or they may be dried and then stored under normal room conditions.

The unit of measurement used to define and compare root systems is to some extent determined by the method used to separate the roots from the soil. Weaver's hand separation method enables accurate scale drawings, photographs and written descriptions to be made as the work proceeds, but is not suitable for more than superficial quantitative measurements for the reason that the roots are not completely freed from soil. The 'soil-block' and 'nail-board' techniques are suitable for both descriptive and quantitative work, but, with the latter, care must be taken to avoid the loss of small roots. The 'soil-block' technique has the advantage that the root system may be divided both vertically and horizontally, or the roots may be suspended in their natural positions in a bath of water while measurements and photographs are made.

The soil sampling methods are not suitable for descriptive work but are very suitable for quantitative measurements, as relatively large numbers of samples can be dealt with. Dry weight has been the most popular measurement owing to its ease of determination and interpretation, but it has the disadvantage that certain functions of the root would appear to be more dependent upon the surface area than upon the mass. Volume, usually determined by the displacement of water, has been used by several investigators and significant positive correlation coefficients between weight and volume have been found in nearly every instance. Length of the roots has also been determined by a few workers, but this is a tedious process owing to the large values obtained. Diameter, tensile strength and other measurements have been made at various times. A combination of two measurements into a single factor has been suggested by Rotmistroff (1908) (length and weight), Pavlychenko (1942) (length and tensile strength), Robinson and Jacques (in press) (weight and diameter), but these coefficients would seem to have only limited applications.

The principles of the methods described apply equally to plants grown in the field and in such containers as pots, boxes and drain-pipes. The relative merits of growing the plants in the field or in containers will depend largely upon the experiment in question. Against the merits of ease of handling and the uniformity obtained with containers must be offset the disadvantages of soil disturbance and lack of room for root expansion. Special containers have been devised for root studies by Sachs (1874), Rotmistroff (1908), Obermayer (1939), Crider (1955) and many others.

No technique has yet been devised to enable 'living' roots to be distinguished, with certainty,

from 'dead' ones. Most experimenters have, therefore, included living roots and dead ones not sufficiently decomposed to be unrecognisable in the same category. Čepikova (1942) used the activity of the enzyme catalase and the volume of colloids in the roots to distinguish between living and dead roots, while Stuckey (1941) used the presence of dividing cells at the root-tip to separate growing from non-growing roots. Goedewaagen (1954 and 1955, personal communication) has used tetrazolium chloride in an attempt to distinguish between active and non-active roots while Schwass and Jacques (in press) have used 2, 3, 5, triphenyl tetrazolium bromide for the same purpose. Both these substances are reduced by enzymes in active tissue to produce a coloured precipitate, and this colouration was noted in white roots to varying degrees by both workers. These stains do not appear to be suitable for older roots. Another staining method has been described by Tanašev (1940). Greenham and Cole (1949), with large roots of non-gramineous species, have evolved a method of distinguishing between living and dead roots which depends upon electrical resistance.

Special techniques have been developed by numerous investigators for the study of specific problems. Jacques and Edmond (1952) mounted plants on domes of plaster of Paris sunk into the soil to enable roots to be amputated soon after they were formed. Both Jacques and Edmond, and Crider (1955) have surrounded roots by sphagnum moss to facilitate observation of their growth; the moss was removed when it was necessary to view the roots. Crider also covered the surfaces of roots with carbon black so as to enable the white apical growth to be detected. Russian workers have developed staining techniques for determining the areas, lengths and diameters of roots (Kolosov, 1939, 1942; Tanašev, 1941).

A 'bleeding' technique has been used by Goedewaagen (1955, personal communication) to investigate the ability of a root to absorb and conduct water. The roots to be studied were obtained in a core of soil in which they were growing and the upper ends of the roots exposed. The soil was then wetted to field capacity and kept in an atmosphere of high humidity. At stated intervals it was noted if a drop of liquid had formed on the exposed end of the root; if so the size of the drop was measured and removed. After some days the relative activity of the individual roots was known. The roots were then washed free from soil and studied morphologically.

New techniques are being investigated, the potentialities of which are not yet known. Haaløv and Weis-Fogh (1952–3) have described a microscopic method for studying undisturbed soil which has a possible application to the study of soil/root relationships. The use of radio-active tracer materials in the study of grass roots is still in its infancy but reports of the first work are becoming available (Burton, De Vane and Carter, 1954; Chamblee, Woodhouse and Hall, 1952). The use of 'inert' indicator materials, e.g. lithium, is another possible line of approach yet to be fully investigated (Sayre and Morris, 1940).

Underground organs other than roots may be studied using the same methods as those described above, but, as the organs are not so deeply buried in the soil as the roots, the task is much easier. Normally they are studied in conjunction with the roots.

APPENDIX

Weight of roots (lb. dry or air-dry material per acre) produced by swards

Authority	Location	Age of sward (yr.)	Depth of measurement (in.)	Management	Species	Weight Minimum (lb.)	Weight Maximum (lb.)	Mean (lb.)
				EUROPE				
Hlubeck, cited by Johnston, 1844	Austria	4	—	Hay	*Phleum pratense*			4,114
		,,	—	,,	*Festuca elatior*			5,324
		,,	—	,,	*Dactylis glomerata*			5,445
		,,	—	,,	*Alopecurus pratensis*			5,808
		,,	—	,,	*Lolium perenne*			12,100
		,,	—	,,	*Agropyron repens*			16,940
		,,	—	,,	*Festuca ovina*			19,360
		,,	—	,,	—	3,702	37,249	
Wallin, 1935	Sweden	—	3·9	Pasture	*Lolium/Cynosurus* type			1,942
Klapp, 1943	Germany, Bonn	—	3·94	Park sward	*Dactylis glomerata*			2,970
		5	,,	,, ,,	*Lolium perenne*			2,456
		6–7	,,	Grazed	*Poa pratensis*			5,712
		,,	,,	,,	*Lolium/Poa*			6,140
		,,	,,	,,	*Trifolium repens*			7,240
		,,	,,	,,	*Holcus lanatus*			4,512
	Rengen	—	,,	Heavily grazed and developed from heath by manuring	*Agrostis vulgaris*			4,627
		—	,,		*Festuca rubra*			4,698
		—	,,		*Dactylis glomerata*			4,927
		—	,,		*Cynosurus cristatus*			5,541
		—	,,		*Poa trivialis*			5,583
		—	,,		*Calluna vulgaris*			5,855
		—	,,	*Calluna/ Antennaria* association	*Nardus stricta*			7,254
		—	,,		*Anthoxanthum odoratum/ Festuca ovina*			7,697
		—	,,		*Holcus mollis*			7,897
		—	,,	Boggy areas in above association	*Deschampsia caespitosa*			10,610
Bates, 1948	England	1–7	6	Normal farm practice	Leys; predominantly *Lolium perenne*	1,429	18,353	
Salonen, 1949	Finland	1	22	—	*Phleum pratense* + *Trifolium pratense*	1,517	8,859	
		2	,,	—	,, — ,,	2,217	17,820	
		Old	,,	—	—	6,557	18,470	
Goedewaagen and Schuurman, 1950a	Netherlands	—	8	Survey	—	2,052	9,815	6,245
Troughton, 1951	Wales	Old	6	Grazed and cut for hay	*Lolium perenne, Agrostis* spp. & *Poa* spp. (includes some leaf bases)	11,880	19,325	
		,,	,,			13,778	20,888	

Authority	Location	Age of sward (yr.)	Depth of measurement (in.)	Management	Species	Weight Minimum (lb.)	Weight Maximum (lb.)	Mean (lb.)
Kmoch, 1952	Germany	—	11·8	Survey	*Poa trivialis*			2,640
		—	,,	,,	*Lolium multiflorum*			4,762
		—	,,	,,	*Trifolium repens*			4,993
		—	,,	,,	*Lolium perenne*			5,038
		—	,,	,,	*Poa pratensis*			6,126
		—	,,	,,	*Festuca pratensis*			6,511
		—	,,	,,	*Arrhenatherum elatius*			6,627
		—	,,	,,	*Holcus lanatus*			10,014
		—	,,	,,	*Dactylis glomerata*			10,501
		—	,,	,,	*Festuca rubra*			11,337
		—	,,	,,	*Agrostis vulgaris*			12,654
		—	,,	,	*Agrostis alba*			13,116
		—	,,	,,	*Phleum pratense*			13,449
		—	,,	,,	*Festuca arundinacea*			13,597
		—	,,	,,	*Deschampsia caespitosa*			16,613
		—	,,	,,	*Bromus erectus*			18,752
		—	,,	,,	*Nardus stricta*			21,694
		—	,,	,,	*Phalaris arundinacea*			32,178
		—	,,	,,	*Molinia caerulea*			42,252
Schuurman, 1954	Netherlands	1	3·9	Moderate utilization	*Trifolium repens*			1,010
		,,	,,		*Agrostis stolonifera*			1,380
		,,	,,	,,	*Poa trivialis*			1,590
		,,	,,	,,	*Phleum pratense*			1,750
		,,	,,	,,	*Poa pratensis*			2,300
		,,	,,	,,	*Cynosurus cristatus*			2,370
		,,	,,	,,	*Lolium perenne* (hay strain)			2,790
		,,	,,	,,	*Festuca pratensis* (grazing strain)			2,990
		,,	,,	,,	*Lolium perenne* (grazing strain)			3,200
		,,	,,	,,	*Festuca rubra*			3,570
Kübler, 1954	Germany	—	8	—	*Dactylis glomerata*			2,194
		—	,,	—	*Phleum pratense*			2,703
		—	,,	—	*Arrhenatherum elatius*			2,730
		—	,,	—	*Lolium perenne*			3,461
		—	,,	—	*Poa pratensis*			4,219
Baker, H. K., 1955	England	1·5	9	Defoliation treatments	*Lolium perenne*		5,520	
Simon and Eich, 1955	Germany	1·5	—	—	*Festuca ovina*			6,581
		2·25	—	—	,, ,,			9,430
		1·25	8	—	*Trisetum flavescens*			5,581
		1·25	—	—	,, ,,			2,825
		0·5	8	—	,, ,,			5,648

Authority	Location	Age of sward (yr.)	Depth of measurement (in.)	Management	Species	Weight Minimum (lb.)	Weight Maximum (lb.)	Mean (lb.)
		0·5	8	—	,, ,,			3,616
		1·5	8	—	,, ,,			3,934
		1·75	12		,, ,,			9,350
		1·25	8	—	*Dactylis glomerata*			5,230
		1·25	—	—	,, ,,			4,374
		1·5	8	—	,, ,,			4,565
		1·5	8	—	*Lolium italicum*			3,192
		0·5	8	—	*Festuca rubra*			2,980
		0·5	8	—	,, ,,			8,184
		1·5	8	—	,, ,,			6,460
		0·5	8	—	,, ,,			2,975
		2·5	8	—	,, ,,			6,490
				UNITED STATES OF AMERICA				
Woods, 1889	Connecticut	—	24	—	*Phleum pratense*			2,516
Trowbridge, Haigh and Moulton, 1915	Missouri	—	—	Uncut	*Phleum pratense* (roots & stubble)	821	1,095	
Graber, Nelson, Leukel and Albert, 1927	Wisconsin	1–3	Sod	—	*Poa pratensis* (roots & rhizomes)	4,992	7,968	
Laird, 1930	Florida	—	40	Pasture	*Cynodon dactylon*			2,308
		4	,,	Lawn	,, ,,			989
		—	,,	Pasture	*Stenotaphrum secundatum*			2,583
		—	,,	Lawn	,, ,,			3,160
		—	,,	Pasture	*Eremochloa ophiuroides*			4,727
		—	,,	Lawn	,, ,,			5,661
		—	,,	Pasture	*Paspalum notatum*			6,156
		—	,,	Lawn	,, ,,			6,705
		4	,,	Pasture	*Axonopus compressus*			3,435
		4	,,	Pasture	*Digitaria didactyla*			1,484
		—	,,	Lawn	*Paspalum dilatatum*			5,139
Sturkie, 1930	Alabama	<1	—	Various defoliation treatments	*Sorghum halepense*	48	6,159	
Willard and McClure, 1932	Ohio	1	6	Defoliation treatments	*Poa pratensis*	480	4,380	
		2	,,		,, ,,	2,640	4,030	
Sprague, H. B., 1933	New Jersey	4	9	Defoliated weekly	*Agrostis canina*			4,613
		,,	,,		,, *tenuis*			4,639
		,,	,,	,,	,, *alba*			5,432
		,,	,,	,,	,, *palustris*			5,654
		,,	,,	,,	*Festuca ovina* var. *duriuscula*			6,111
		,,	,,	,,	*Poa pratensis*			7,588
Weaver and Harmon, 1935	Nebraska	—	12	Prairie (lowland)	*Poa pratensis*			6,615
		—	,,	Prairie (upland)	*Poa pratensis*			6,496
		—	,,	Prairie	*Stipa spartea*			6,196

Authority	Location	Age of sward (yr.)	Depth of measurement (in.)	Management	Species	Weight Minimum (lb.)	Weight Maximum (lb.)	Mean (lb.)
		—	,,	,,	*Bouteloua gracilis*			7,475
		—	,,	,,	*Bulbilis* (*Buchloë*) *dactyloides*			7,553
		—	,,	,,	*Andropogon scoparius*			10,031
		—	,,	,,	*Andropogon furcatus*			12,251
		—	,,	,,	Early stage prairie (upland)			6,814
		—	,,	,,	Medial ,, ,, ,,			6,436
		—	,,	,,	Late ,, ,, ,,			2,919
		—	,,	,,	Early ,, ,, (lowland)			8,534
		—	,,	,,	Medial ,, ,, ,,			6,973
		—	,,	,,	Late ,, ,, ,,			2,916
Gernert, 1936	Oklahoma	—	5	Survey	*Andropogon* sp. *Panicum* sp. *Sorghastrum* sp. *Bouteloua* sp., etc.	3,719	20,247	9,514
Weaver, Hougen and Weldon, 1935	Nebraska	—	48 and 84	Prairie	*Andropogon scoparius* *Andropogon furcatus* mainly	10,947	15,775	
Kramer and Weaver, 1936	Nebraska	Old	4	Pasture	*Poa pratensis*			4,800
		,,	,,	Prairie	*Spartina michauxiana*			13,240
Hughes, 1937	Iowa	4	12	Defoliation treatments	*Poa pratensis*			
					roots	1,933	2,839	
					rhizomes	629	1,127	
Shively and Weaver, 1939	Nebraska	—	3·94	Prairie	*Andropogon scoparius*	4,192	7,582	
		—	,,	,,	*Andropogon furcatus*	5,655	10,829	
		—	,,	,,	Mixed *Andropogon*	4,817	8,813	
		—	,,	,,	*Agropyron smithii*	1,338	5,923	
		—	,,	,,	*Bouteloua gracilis*	2,159	6,440	
		—	,,	,,	*Buchloë dactyloides*	2,837	6,654	
Hanson and Stoddart, 1940	Utah	Aged	23·6	Grazed	*Agropyron smithii*			2,260
		,,	,,	Protected	,, ,,			13,850
Watkins, 1940	Ohio	1	6	Infrequently defoliated	*Bromus inermis*			
					roots	1,370	2,570	
					rhizomes	80	90	
Pavlychenko, 1942	Nebraska	Established	3·94	Prairie	*Bouteloua gracilis*			2,190
		,,	,,	,,	*Agropyron smithii*			2,586
		,,	,,	,,	*Stipa spartea*			2,742
	Iowa	,,	,,	,,	*Andropogon scoparius*			3,344
	Nebraska	,,	,,	,,	*Sporobolus cryptandrus*			3,809
		,,	,,	Pasture	*Poa pratensis*			4,929
		,,	,,	,,	*Andropogon furcatus*			6,148
Brown, E. M., 1943	Missouri	2–5	6	Defoliation treatments	*Poa pratensis*			
					roots	978	2,704	
					rhizomes	328	15	

Authority	Location	Age of sward (yr.)	Depth of measurement (in.)	Management	Species	Weight Minimum (lb.)	Weight Maximum (lb.)	Mean (lb.)
Haynes, 1943	New Jersey	4	6	Grazed	*Poa pratensis* and *Trifolium repens*	22,360	29,790	
Bell and De France, 1944	Rhode Island	Established	8	Mown thrice weekly	*Agrostis canina*	12,676	14,810	
		,,	,,		,, *palustris*	3,485	7,144	
		,,	,,	,,	,, *tenuis*	4,400	6,011	
Crider, 1945	Maryland	3	12	—	*Eragrostis curvula*			6,634
		,,	,,	—	*Andropogon furcatus*			6,441
		,,	,,	—	*Andropogon scoparius*			6,340
		,,	,,	—	*Bouteloua gracilis*			3,204
		,,	,,	—	*Bouteloua curtipendula*			2,890
		,,	,,	—	*Festuca elatior*			2,192
		,,	,,	—	*Dactylis glomerata*			1,842
Schwendiman, 1946	Washington	<1	8	Grown for green manure	*Dactylis glomerata* and *Melilotus alba*			3,700
Gist and Smith, 1948	Virginia	3	18	—	*Bromus inermis*			4,186
		,,	,,	—	*Dactylis glomerata*			4,673
		,,	,,	—	*Poa pratensis*			3,832
		,,	,,	—	*Phleum pratense*			2,296
		Aged	,,	—	*Panicum clandestinum*			14,966
Kennedy and Russell, 1948	New York	6	3	Cut every week for 6 years	*Poa pratensis*			4,180
		—	,,	Uncut for 7 years	,, ,,			6,960
Lamba, Ahlgren and Muckenhirn, 1949	Wisconsin	0·5	16	—	*Bromus inermis*			1,869
		1·0	,,	—	,, ,,			4,112
		0·5	,,	—	*Phleum pratense*			1,064
		1·0	,,	—	,, ,,			3,356
Ward, 1949	Iowa	7	18	—	*Andropogon furcatus*			13,344
		,,	,,	—	*Panicum virgatum*			9,319
		,,	,,	—	*Sorghastrum nutans*			10,522
		,,	,,	—	*Poa pratensis*			7,213
Weaver and Darland, 1949	Nebraska	—	60	Prairie	*Andropogon furcatus*	8,388	26,163	
		—	Maximum.	,,	*Andropogon scoparius*	20,381	23,282	
		—	Samples	,,	*Bouteloua curtipendula*	11,108	15,302	
		—	taken to	,,	*Poa pratensis*	3,308	10,841	
		—	maximum	,,	*Agropyron smithii*	4,895	7,549	
		—	depth of	,,	*Bouteloua gracilis*	3,484	14,016	
		—	rooting	,,	*Buchloë dactyloides*	4,437	10,594	
		—	,,	,,	*Panicum virgatum*			22,412
Weaver, 1950	Nebraska	—	48	Prairie	Mixed	5,370	12,900	
		—	,,	,,	*Andropogon scoparius*	2,000	7,940	
		—	,,	,,	*Andropogon furcatus*	1,466	5,627	
Weaver and Voigt, 1950	Nebraska	—	72	Prairie	*Andropogon furcatus*			13,993
		—	36	,,	*Poa pratensis*			8,536

Authority	Location	Age of sward (yr.)	Depth of measurement (in.)	Management	Species	Weight Minimum (lb.)	Weight Maximum (lb.)	Mean (lb.)
Albertson, Riegel and Launchbaugh, 1953	Kansas	Aged	84	Defoliation treatments	*Bouteloua gracilis* and *Bulbilis dactyloides*	5,527	12,440	8,740
Hopkins, 1953	Kansas	Native.	48	Normal practice	*Buchloë dactyloides*			11,428
		Natural re-vegetation	,,	,,	,, ,,			5,277
		9	,,	,,	*Bouteloua gracilis*			16,100
		3	,,	,,	,, ,,			9,746
		5	,,	,,	*Andropogon gerardii*			20,270
		9	,,	,,	*Panicum virgatum*			21,220
		2	,,	,,	,, ,,			3,549
		8	,,	,,	*Bouteloua curtipendula*			10,680
		Native	,,	,,	*Agropyron smithii*			8,454
		2	,,	,,	,, ,,			3,630
		Natural re-vegetation	,,	,,	*Sporobolus cryptandrus*			2,282
		5	,,	,,	*Poa pratensis*			6,488
		2	,,	,,	*Bromus inermis*			3,100
Schwendiman, Hafenrichter and Law, 1953	Washington	1	8	—	*Melilotus alba*			
		,,	,,	—	+ *Arrhenatherum elatius*			1,926
		,,	,,	—	+ *Agropyron trachycaulum*			1,770
		,,	,,	—	+ *Agropyron cristatum*			2,285
		,,	,,	—	+ *Bromus marginatus*			2,308
		,,	,,	—	+ *Dactylis glomerata*			2,531
		,,	,,	—	Average			2,173
Woods, Hafenrichter, Schwendiman and Law, 1953	Washington	4	8	Hay	Average of 20 species plus *Medicago sativa*			9,720
Burton, De Vane and Carter, 1954	Georgia	2	96	Clipped thrice yearly	*Cynodon dactylon*			5,569
		,,	,,		*Paspalum notatum*			9,250
Rice and Penfound, 1954	Oklahoma	—	7	Prairie	*Andropogon* spp.			5,113
				SOUTH AMERICA				
Villares, Tundisi and Becker, 1953	Brazil	Aged	88	Pasture	*Panicum maximum*			2,531
Ampson, 1954	Dutch Guiana	2	24–47	Defoliation treatments	*Paspalum notatum*	5,342	13,882	
				CANADA				
Pavlychenko, 1942	Saskatchewan	2	59·8	—	*Agropyron pauciflorum*			3,011
		4	,,	—	,, ,,			3,111
		2	,,	—	*Agropyron cristatum*			4,200
		4	,,	—	,, ,,			8,355
		2	,,	—	*Bromus inermis*			4,517
		4	,,	—	,, ,,			5,969

Authority	Location	Age of sward (yr.)	Depth of measurement (in.)	Management	Species	Weight Minimum (lb.)	Weight Maximum (lb.)	Weight Mean (lb.)
				AFRICA				
Coetzee, Page and Meredith, 1946	South Africa	Aged	24	—	High veld			13,494
Weinmann, 1948c	Johannesburg	—	6	Grazed	*Trachypogon plumosus and Tristachya hispida* dominant	753	2,638	
Weinmann and Goldsmith, 1948	Frankenwald	7	6·5	Defoliation treatments	*Cynodon dactylon*:			
					roots	8,780	19,720	
					rhizomes	9,220	13,580	
Weinmann, 1949	Southern Rhodesia	—	4	Defoliation treatments	Sandveld grasses	70	398	
Bartholomew, Meyer and Laudelout, 1953	Belgian Congo	3	—	—	*Setaria sphacelata*			6,870
		,,	—	—	*Panicum maximum*			8,780
		,,	—	—	*Cynodon dactylon*			10,750
				RUSSIA				
Nad'jarnyĭ, 1939	—	—	15·9	Hayed	*Phleum pratense*			2,712
		—	,,	,,	*Agropyron cristatum*			3,399
		—	,,	,,	*Dactylis glomerata*			4,211
		—	,,	,,	*Bromus inermis*			4,514
		—	,,	,,	*Arrhenatherum elatius*			4,630
		—	,,	,,	*Agropyron tenerum*			6,022
		1–3	—	—	*Bromus inermis*	1,900	3,417	
Ivanov, 1950	—	Perennial ?	9	—	Grasses and legumes	3,628	13,603	
				CEYLON				
Haworth, 1952		3	120	—	*Tripsacum laxum*			44,800
Haworth, 1953		1	6	—	*Axonopus compressus*			6,720
		1	6	—	*Pennisetum purpureum*			8,960
		4	6	—	,, ,,			4,480
		2	10	—	*Tripsacum laxum*			43,008
		2	6	—	,, ,,			13,992
		3	6	—	*Paspalum urvillei*			11,872
		Old	6	—	*Andropogon nutans* association			11,872
				NEW ZEALAND				
Campbell, 1945	Hawkes Bay	Aged	8	Good pasture				7,734
		,,	,,	,, ,,				9,535
		,,	,,	Poor ,,				512
		,,	,,	Ungrazed pasture				11,860

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